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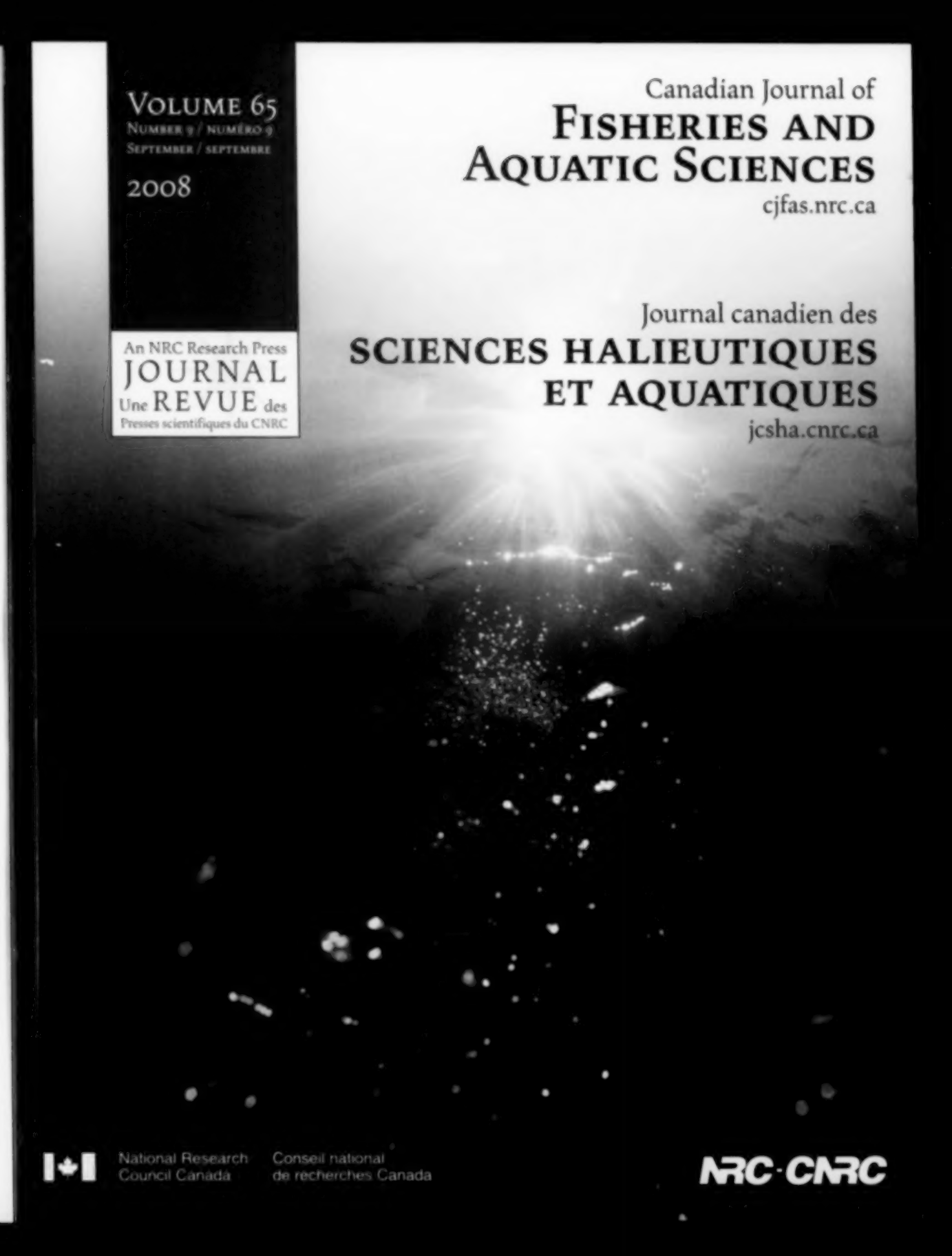

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RAPID COMMUNICATION / COMMUNICATION RAPIDE

Postconsumption domoic acid generation by the diatom *Pseudo-nitzschia multiseries* as a factor in depuration models

James E. Stewart

Abstract: A theoretical analysis of the clearance of the neurotoxin domoic acid (DA) from molluscan shellfish, notably the blue mussel (*Mytilus edulis*), indicated that the depuration simulation did not account for the maximum accumulation of DA nor for the failure to eliminate all of the DA from the mussels in the anticipated time. Subsequent examination of relatively young, neurotoxin-producing cells of *Pseudo-nitzschia multiseries* concentrated 8.5- to 10-fold and reincubated in the dark, however, showed significant amounts of DA were produced within the first 24 h of incubation. The possible production of DA, after ingestion, could generate an additional contribution to the toxin burden in the mollusc, which, when included in the depuration simulation, would explain part or all of the observed disparity in the depuration experiment.

Résumé : Une analyse théorique de la clearance de l'acide domoïque (DA), une neurotoxine chez les mollusques comestibles, particulièrement chez la moule bleue (*Mytilus edulis*), indique que la simulation de la dépuration n'explique pas l'accumulation maximale de DA, ni le fait que la totalité de DA n'est pas éliminée des moules dans le temps prévu. Un examen subséquent de cellules productrices de neurotoxine relativement jeunes de *Pseudo-nitzschia multiseries*, concentrées par un facteur de 8,5 à 10 et incubées de nouveau à l'obscurité, montre qu'il y a une production d'importantes quantités de DA durant les premières 24 h de l'incubation. La production possible de DA après l'ingestion pourrait ajouter une contribution supplémentaire à la charge de toxine du mollusque qui, une fois incluse dans la simulation de dépuration, expliquerait en totalité ou en partie la disparité observée au cours de l'expérience de dépuration.

[Traduit par la Rédaction]

Because the accumulation of the neurotoxin domoic acid (DA) and other algal toxins in molluscan shellfish interferes markedly with commercial fisheries, toxin depuration has assumed greater importance. Unfortunately, depuration is not a simple, universal process. Some species sequester the toxins firmly for lengthy periods, while others rid themselves of the toxins readily and more or less completely.

For example, studies on the clearance of DA have shown that scallops (*Placopecten magellanicus* and *Pecten maximus*) retain elevated concentrations of the toxin, largely in the digestive gland, for extended periods (Scarratt et al. 1991; Blanco et al. 2006). In one set of depuration trials, retention of DA by *Placopecten magellanicus* was recorded as essentially unchanged in the digestive gland for periods up to 19 months (Stewart et al. 1998). It is probable that scallops retain DA and other toxins such as paralytic shellfish poisons (PSP) (Waiwood et al. 1995) through compartmentalization or bonding with tissue-specific, high- and low-affinity receptor sites as noted by Trainer and Bill (2004) for razor clams (*Siliqua patula*), which they suggest allow the razor clam to retain and tolerate high levels of DA. In contrast, blue mussels (*Mytilus edulis*) clear the DA burden and PSP toxins readily and rapidly (i.e., within days), dependent to a considerable extent upon temperature (Scarratt et al. 1991; Silvert and Subba Rao 1992).

To gain an improved understanding of depuration, Silvert and Subba Rao (1992) developed a single compartment model of the DA flux through an *M. edulis* population and suggested that theoretical analyses of such models could be useful tools for testing assumptions underlying the management of shellfish fisheries. Their simulation was based on information drawn from laboratory measurements that included filtering volumes and depuration rates for individual mussels and the premise that *M. edulis* ingests DA only in particulate form (i.e., in the diatom cells) and does not assimilate extracellular, excreted, dissolved DA. This simulation, however, could not account for the peak levels (200–300 μg DA·g^{-1} wet weight of mussel soft tissue) recorded for the 1988 bloom in Cardigan Bay, Prince Edward Island, Canada (Bates et al. 1989). In attempting to explain the dis-

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Table 1. Production of domoic acid by concentrated *Pseudo-nitzschia multiseries* cell suspensions incubated in the dark.

Domoic acid in filtrates (ng·mL^{-1}) after concentration				
0 h	4 h	24 h	28 h	48 h
10-day growth*				
150.0±28.9	117.8±33.4	180.0±37.3	414.4±90.8	—
5-day growth†				
150.0±28.9	—	833.3±120.2	—	700.0±57.7

Note: Filtrates result from sonic treatment of samples of the concentrated *P. multiseries* suspensions ± standard error (SE), $n = 3$.

*Concentration of the nonaxenic initial *P. multiseries* culture cell mass (200 535 ± 9 564 cells·mL^{-1}) 8-fold produced a final cell count of 1 604 000 cells·mL^{-1}.

†Concentration of the nonaxenic initial *P. multiseries* culture cell mass (161 402 ± 12 028 cells·mL^{-1}) 10.5-fold produced a final cell count of 1 695 000 cells·mL^{-1}.

parity they considered several alternatives, including (*i*) increased grazing rates during bloom conditions, (*ii*) a drastic decrease in depuration rates under bloom conditions via a physiological response in the mussel that interferes with depuration, or (*iii*) some microbial or other internal mechanism that leads to the production of DA in the gut of the mussel. As the laboratory measurements available to them ruled out only the first alternative, the question concerning the disparity was left open.

Subsequent to the studies of Silvert and Subba Rao (1992), Stewart et al. (1998) provided data that was relevant to the second alternative by showing that DA and its analogue, kainic acid, were highly refractory to many bacteria. Commonly, however, isolations from mussels (*M. edulis*) and softshell clams (*Mya arenaria*) routinely produced bacteria capable of growing at the expense of DA. These bacteria were comparable to those isolated from associations with the diatom *Pseudo-nitzschia multiseries*, which, in fact, might be their source. Bacteria isolated from associations with the diatom also had been shown to be capable of growing at the expense of DA. In addition, Stewart (2008) demonstrated that *P. multiseries* in axenic culture did not utilize DA, but the associated bacteria separated from the diatom utilized it readily. Thus there is a high probability that much or possibly all of the digestion and clearance of DA from blue mussels is conducted by bacteria. If the depuration of DA is largely or wholly bacterial, it is possible that accumulating high concentrations of DA could have a negative effect on the depuration. As Stewart et al. (1998) showed, DA levels of 0.8–1.6 μmol DA·mL^{-1} inhibited the endogenous respiration of *Pseudomonas* and *Alteromonas* species and that even DA-utilizing bacteria grown at 40 nmol DA·mL^{-1} for 6 days at 20 °C did not eliminate all of the DA presented (Stewart 2008). These data raise the possibility that high concentrations of DA could slow DA clearance, at least initially, until the relevant bacterial populations, along with suitable conditions, were enhanced appreciably.

The third alternative that proposed some microbial or other mechanism might lead to production of DA in the gut of the mussel following ingestion of *P. multiseries* was examined partially by a simple simulation as follows. The diatom, *P. multiseries* (strain NPH), was grown nonaxenically in bulk in two separate trials under the standard conditions described in Stewart et al. (1997). The diatom was harvested by low speed centrifugation (<300*g*) while the cultures were still in the exponential stages (10 and 5 days), where the DA formation would be very low or none (Bates 1998; Stewart 2008). The resting cells, handled aseptically throughout, were resuspended in the original, partially spent, clarified growth medium at 8- and 10.5-fold their original concentrations and dispensed in triplicate. To more fully simulate activity in the mussel gut, the highly concentrated diatoms were then incubated in the dark at the original growth temperature (20 °C) for the periods indicated (Table 1). Samples were withdrawn at intervals, and the cells were examined microscopically. Interestingly, the diatom cells remained intact and in apparent good condition throughout the dark incubation periods. The whole sample (containing the resting cells) was then treated sonically (1 min at 35% power; Sonic Dismembrator-Artek System) to rupture the cells; the DA in the resulting clarified filtrates was measured by the ELISA method of Osada et al. (1995). The results show that the resting cells did produce DA in the dark and that in these trials the younger cells (5-day growth) produced the largest quantities of DA (i.e., 833 ng DA·mL^{-1}) within 24 h (Table 1). The net value for this 24 h production (833 ng·mL^{-1} minus the zero time value of 150 ng·mL^{-1} = 683 ng·mL^{-1}) divided by the diatom cell population that produced it (i.e., 683 ng DA·(1 695 000 cells·mL^{-1})$^{-1}$) showed that each diatom cell contributed 0.4029 pg to the total. These data suggest that the third alternative suggested by Silvert and Subba Rao (1992) is possible and probable (i.e., the diatom cells consumed by the mussel (essentially intact resting cells awaiting digestion) could continue to produce substantial amounts of DA in the dark).

In their simulation, Silvert and Subba Rao (1992) based their calculations on grazing rate experiments using diatom concentrations of 0.52×10^6 to 11.64×10^6 cells·L^{-1}, which they concluded reflected the natural situation. These rates indicated "that at these concentrations the filtration rates of the size of mussels found in Cardigan Bay (6.5 g) would be approximately 40 L·mussel^{-1}·day^{-1}" (Silvert and Subba Rao 1992).

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Application of the maximum net production of DA per cell (0.4 pg·cell^{-1}) recorded for the resting cells (Table 1) to the lower and upper diatom cell numbers Silvert and Subba Rao (1992) used in their simulation suggests a possible explanation for the disparity they observed:

(1) Silvert and Subba Rao's lower value of 0.52×10^6 diatom cells · L^{-1}:

$$0.52 \times 10^6 \text{ diatom cells} \cdot \text{L}^{-1} \times 40 \text{ L filtered seawater} \cdot \text{mussel}^{-1} \times 0.4 \text{ pg DA} = 8.32\ \mu\text{g DA} \cdot 6.5\ \text{g}^{-1} \text{ mussel}$$

(2) Silvert and Subba Rao's upper value of 11.64×10^6 diatom cells · L^{-1}:

$$11.64 \times 10^6 \text{ diatom cells} \cdot \text{L}^{-1} \times 40 \text{ L filtered seawater} \cdot \text{mussel}^{-1} \times 0.4 \text{ pg DA} = 186.24\ \mu\text{g DA} \cdot 6.5\ \text{g}^{-1} \text{ mussel}$$

As the soft body tissue of a mussel is approximately 40% of its total weight (2.6 g in the case of 6.5 g mussels), the potential contribution to the DA burden in each mussel would be between 8.32 μg DA·2.6 g^{-1} (or 3.2 μg DA·g^{-1} mussel soft body tissue) for the lower diatom cell concentration and 186.24 μg DA·2.6 g^{-1} (or 71.63 μg DA·g^{-1} mussel soft body tissue) for the upper diatom cell concentration. Thus, if the maximum resting cell production was added to the overall mussel body burden calculated by Silvert and Subba Rao (1992) to be 300 μg DA·g^{-1} of soft tissue, the amount of DA to be depurated would actually have been 371.63 μg DA·g^{-1} of mussel soft tissue (i.e., around 24% greater than the amount they considered).

As there is a very real possibility that depuration of DA by the blue mussel is partly or wholly bacterial, an initial lag in depuration could be expected when very high levels of DA are present (e.g., 300 μg DA·g^{-1} or even much higher, such as the 900 μg DA·g^{-1} soft body tissue observed by Quilliam et al. (1989)). These levels could prove inhibitory to bacterial depuration, at least at first. This possibility, plus an hitherto uncounted DA contribution from ingested, resting diatom cells, would be sufficient to explain the disparity in the buildup and depuration of DA in mussels observed by Silvert and Subba Rao (1992) and in fact are in accord with the second and third alternatives suggested by them to account for the disparity.

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Do North Sea cod (*Gadus morhua*) fisheries maintain high catch rates at low stock size?

Anna Rindorf and Bo Sølgaard Andersen

Abstract: This study presents an investigation of the relationship between stock size of North Sea cod (*Gadus morhua*) and catch rates in seven commercial fishing fleets. The shape of the relationship was estimated using a new model allowing both density-dependent changes in catchability and bias in the assessment biomass estimates. Catchability in fisheries targeting a mixed species composition either remained constant or decreased with decreasing stock size, whereas catchability in targeted cod fisheries increased with decreasing stock size. However, even in the cases where catchability increased, the change was insufficient to compensate for the decrease in stock size, and catch rates of all fleets decreased. Two factors that could lead to nonconstant catchability were investigated: (*i*) the presence of a decoupling between stock size and density in high-density areas and (*ii*) the presence of concurrent shifts in the spatial distribution of the cod stock and the cod fishery. No evidence of the former was found, but there was a northern shift in the spatial distribution of both effort and the cod stock.

Résumé : Notre travail étudie la relation entre la taille du stock de morues (*Gadus morhua*) de la mer du Nord et les taux de capture de sept flottes de pêche commerciale. La forme de la relation a été estimée à l'aide d'un nouveau modèle qui tient compte des changements de capturabilité dépendants de la densité et d'erreurs dans les évaluations des estimations de biomasse. Dans les pêches commerciales qui ciblent un mélange d'espèces, la capturabilité reste constante ou diminue avec le déclin de la taille du stock, alors que, dans les pêches qui ciblent la morue, elle augmente lorsque la taille du stock diminue. Cependant, même dans les cas d'augmentation de la capturabilité, ce changement ne suffit pas à compenser le déclin de la taille du stock; les taux de capture des toutes les flottes diminuent donc. Nous avons examiné deux facteurs qui pourraient expliquer pourquoi la capturabilité ne reste pas constante: (*i*) soit l'existence d'un découplage entre la taille du stock et la densité dans les zones de forte densité et (*ii*) la présence de déplacements concomitants des répartitions spatiales du stock de morues et de la pêche commerciale à la morue. Nous ne trouvons aucune indication de l'existence du premier facteur, mais il y a un déplacement vers le nord de la répartition de l'effort de pêche et de celle du stock de morues.

[Traduit par la Rédaction]

Introduction

The stability of any exploited stock relies on the relationship between stock size and harvest rate. If harvest rate decreases with declining stock size, year-to-year variation in stock size is decreased and limited harvesting has a stabilizing effect. In contrast, if harvest rate increases with declining stock size, any decrease in stock size is aggravated as the stock is further diminished by exploitation, and the probability of collapse of the stock is increased. Harvest rate in fish stocks is usually regulated by restricting total landings, effort exerted, and a number of technical measures such as gear type and mesh size. The restriction of fishing effort is based on the implicit assumption that catchability is constant. However, catchability in several fisheries increases with decreasing stock size (Rose and Leggett 1991; Rose and Kulka 1999; Swain et al. 1994), presumably by targeting local areas where density remains high (Paloheimo and Dickie 1964; Crecco and Overholtz 1990; Rose and Leggett 1991). The increase in catchability often leads to an increase in harvest rate, as catch rate remains high (hyperstable) at low stock size, giving the fishing fleet the potential to destabilize a small stock further. Knowledge of the presence or absence of a relationship between stock size and catchability is thus crucial when attempting to predict the effect of different effort management measures, a task that is required on a yearly basis for a great number of exploited stocks. Accuracy in the predictions is particularly important at low stock sizes, a situation in which data quality may be deteriorating because of misreporting and low catch rates in surveys.

A stock that is currently at a historic low owing to the combined effect of fishing and changing climatic conditions is the North Sea cod (*Gadus morhua*) stock (O'Brien et al. 2000; Beaugrand et al. 2003; ICES 2006). In addition to the severe decline in stock size, the stock has exhibited changes in spatial distribution and is now distributed more northerly than previously (Perry et al. 2005; Rindorf and Lewy 2006). Furthermore, the area inhabited by juvenile cod seems to have contracted as stock size decreased (Blanchard et al.

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2005). The stock would thus appear to have the potential to exhibit a highly undesirable combination of decreasing stock size and increasing catchability because of a contraction and change in location of the inhabited area. However, it has not yet been investigated whether catchability in the commercial fisheries has actually changed or whether any changes can be linked to a relatively constant density of cod in high-density areas. This problem is particularly relevant as catch rates of cod are now regulated through limitations of both total catch and effort.

The objective of this study was to investigate the relationship between stock size and catchability of North Sea cod. The study was divided into three parts: First, the relationship between stock size and catch rate in seven commercial fisheries was investigated to determine whether catchability changed with stock size. Second, the relationship between the change in the spatial distribution of cod and fishing effort was examined to determine whether cod-related fisheries have followed the northwards shift in distribution of the population or the cod-related fisheries has retained its historic distribution. Finally, the relationship between stock size and survey catch rates in high-density areas was investigated to determine whether the presence of a relationship between catchability and stock size could be explained by constant high densities in these areas.

Materials and methods

Stock size

Stock size of North Sea (ICES areas IV, IIIA, and IIVD) cod is estimated each year by the International Council for the Exploration of the Sea (ICES 2006). The biological assessment is based on reported landings, estimates of discards, and age compositions of both landings and discards. In addition, catch rates in the first and third quarter International Bottom Trawl Surveys (IBTS) are used to tune the assessment. In recent years, concern about the reliability of the reported total landings has led to the adoption of a modified assessment where total landings in the years 2000 to 2005 are adjusted by a yearly factor accounting for unaccounted mortality due to, for example, unreported landings. This factor is determined by a comparison between stock numbers and catch rates in the IBTS. Commercial catch rates are not used to tune the cod assessment, and though they contribute to total landings, it is unlikely that the catch rate of an individual fleet will affect the assessment. Hence commercial catch rates can be compared directly with assessment-derived estimates of stock biomass without introducing a bias in the analyses, whereas catch rates in the IBTS surveys are intrinsically linked to the assessment and therefore cannot be used to determine the actual relationship between stock size and survey catch rates.

Catch and effort data

The catch in numbers per hour of each age group taken by two English fleets (English trawlers and English seiners) were derived from the assessment report (ICES 2006). These catch rates include discard estimates (ICES 2006) and hence provide direct estimates of catches rather than just landings. Estimates of biomass caught per unit effort were derived from catch numbers multiplied by the weight at age in landings (also given in ICES 2006). The catch per unit effort (CPUE) of English trawlers was available for the years from 1978 to 2005, whereas CPUE of English seiners was only available up to 2001. Later years were therefore excluded from the analyses for this fleet. Though CPUE of three Scottish fleets are also given in the reports, previous analyses (Cook and Armstrong 1985) have demonstrated that a historical change in the areas fished has led to severe changes in catchability of Scottish fleets. Hence, the differences seen in catchability are not directly related to stock size, and these fleets were not examined.

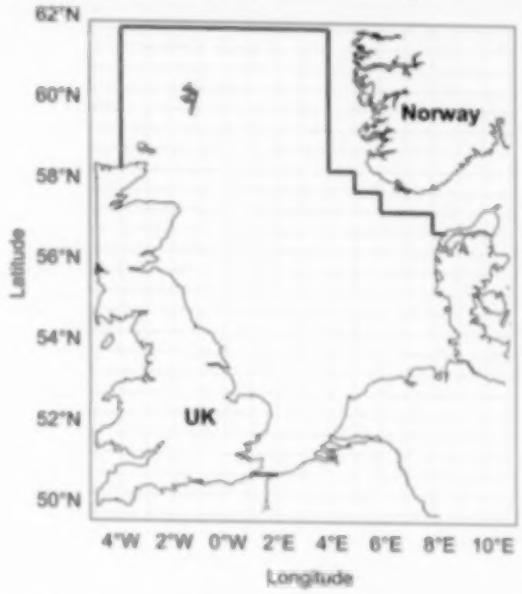

Fig. 1. Study area. Small rectangles are International Council for the Exploration of the Sea (ICES) statistical rectangles.

Effort and cod landings of five Danish fleets (small trawlers, large trawlers, small gillnetters, large gillnetters, and Danish seiners) was estimated from a combination of vessel data, sales slips, and official logbook records. In addition to date and location of each trip, the Danish logbooks provide information on vessel size, gear used, mesh size, weight, and value of landings by species for each ICES statistical rectangle (1 W and 0.5 N, Fig. 1) and number of effort days for each fishing trip. Effort days are defined as days from the first fishing day to the day of entering the landing harbor. Both variables have been mandatory in the Danish logbooks since 1983. As a vessel can fish in several ICES rectangles during a trip, the effort of a trip is allocated to the ICES rectangle from which the highest catches (by value) were taken. Trips and vessels with missing or abnormal information and vessels with income below the economic criteria defining a full-time fisherman were removed from the data set (Ulrich and Andersen 2004). Subsequently, the most important cod-related fleets were defined from a combination of main gear deployed (type and mesh size) and vessel length (Table 1).

The trawl fisheries are mixed species fisheries targeting cod, other demersal fish species, and Norway lobster (*Nephrops norvegicus*), species that are generally caught together.

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Table 1. Definition of Danish cod (*Gadus morhua*) fishing fleets and cod-related fisheries.

Fleet	Vessel length (m)	Gear	Mesh size (mm)	Target species[a]	Avg. % of total Danish cod landings[b]
Small trawlers	0–20	Otter trawl and pair trawl	90–140	—	5%
Large trawlers	20–40	Otter trawl and pair trawl	90–140	—	16%
Small gillnetters	0–20	Gill net and line	90–200	Cod	36%
Large gillnetters	20–40	Gill net and line	90–200	Cod	9%
Seine	All	Danish and Scottish seine	90–150	—	16%

[a]Defined as the most important species by value; —, not defined.
[b]Based on landings statistics from 1990 to 2005.

Including all fishing trips rather than merely trips catching cod has the advantage that trips that do not catch cod owing to low abundance are included. Unfortunately, this means including trips operating in areas where cod could not have been caught even if abundance was high (uninhabitable areas). Though such areas may exist, cod has historically been abundant throughout the North Sea, and uninhabitable areas were therefore considered to be minor, whereas mixed species fisheries had the potential to influence results greatly. Based on these considerations, it was decided to include all trawl and seine fishing trips regardless of whether cod was caught. In contrast with this, the gear type, deployment, and choice of fishing area of the gillnet fisheries depends heavily on which species is the target. The target species or net type is not recorded in the official logbooks, but retrospective analysis of the catch composition indicated that there was a clear separation between catches consisting primarily of cod and catches consisting of flatfish (Ulrich and Andersen 2004). Therefore, a cod-directed fishing trip for the gillnet fleets was defined as a trip where the cod was the dominating species by value (Table 1). These trips covered over 90% of the total cod landings of gillnet fleets. This method assured that catch rates were based on one gear type and deployment only but suffered the disadvantage that low catch rates are likely to lead to a categorization of the trip as non-cod fishery and hence near-zero catch rates are likely to be discarded.

As estimates of discards are unfortunately not available at a disaggregated level for the Danish fleets, the average amount of cod caught per unit effort by a particular fleet in a given year and quarter was estimated as total landings (kg cod) divided by total effort. Only data from the North Sea proper (Fig. 1) in the years 1983 to 2005 were used.

Survey CPUE

The catch at age in numbers per hour in the first quarter IBTS is given in the assessment report (ICES 2006). From this, the total weight of immature and mature cod caught per hour of trawling was estimated by multiplying catch in numbers at age by weight at age in the stock (also available in the assessment report) and maturity at age and then summing over ages. Catch rate of all cod was estimated as the sum of immature and mature fish. In contrast with commercial CPUE series, catch rate in first quarter IBTS was used to tune the assessment (ICES 2006), and this survey is therefore not independent of the assessment. Hence, the correlation between catch per hour in the IBTS was given for comparison, but it was not attempted to estimate changes in catchability, as the assessment was based on an assumption of constant survey catchability (ICES 2006).

Cod density in high-density areas

If cod concentrate in high-density areas as biomass decreases, catch rate in these areas will not be proportional to stock biomass. If these high-density areas are then targeted by the fishery, hyperstability of catch rates will occur. To investigate whether a decoupling of local density and stock size occurred, cod density in high-density areas was estimated from catch rates in the first quarter IBTS (ICES International Bottom Trawl Survey Database 1983–2005: M. Zarecki, ICES, H.C. Andersens Boulevard 44–46, 1553 Copenhagen V, Denmark, personal communication). The survey uses demersal trawls and length composition, and total catch is recorded in each haul. Haul duration generally varies between 0.5 and 1 h, and all catch rates are standardized to hourly values. On average, two trawl hauls are conducted within each ICES statistical rectangle (Fig. 1). Cod age–length keys were estimated using the method suggested by Rindorf and Lewy (2001; Gerritsen et al. 2006; Rindorf et al. 2008). This method uses the correlation between length groups to determine smooth functions between length and the probability of being of a given age and is particularly useful to determine age–length keys in cases with sparse sampling (Rindorf and Lewy 2001), as has been the case with larger cod in recent years. Number of each age group caught per hour was estimated by applying the estimated age–length key to length distributions of the catch. Survey catch rate of mature cod and immature cod within each statistical rectangle (Fig. 1) was estimated by multiplying survey catch rate in numbers at age by weight at age in the stock (given in ICES 2006) and maturity at age (ICES 2006) and then summing over age groups. Total survey catch rate of cod was estimated by summing the catch rate of immature and mature cod.

High-density areas were defined as the 10% of statistical rectangles that supported the highest average survey catch rates in a given year. These areas were selected separately for total and mature cod, and the average total and mature cod survey catch rate within these high-density areas was estimated. Hence, the actual rectangles included were not necessarily the same in all years or for total and mature cod. This method was chosen to avoid the problems caused by using a spatially explicit area while the distribution of the stock is changing and the distribution of immature cod differs from that of mature cod.

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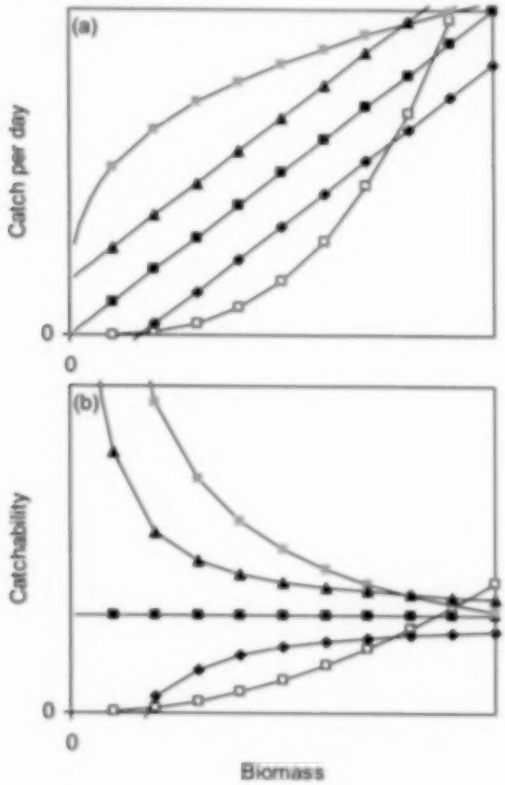
Fig. 2. Relationship between (*a*) catch rate (U) and biomass (B) and (*b*) catchability (U/B) and biomass for different parameterisations of the model $U = aB^{(1+b)} + c$. Solid squares: $b = c = 0$; solid triangles: $b = 0$, $c > 0$; solid diamonds: $b = 0$, $c < 0$; grey squares: $0 < b < 1$, $c = 0$; and open squares: $b > 0$, $c = 0$.



Catch composition

The average proportion of the CPUE of English fleets consisting of mature cod was estimated as the product of catch in numbers, mean weight, and maturity at age as given in ICES (2006) divided by the total catch. The Danish catches were not sampled for age within individual fleets; instead, the distribution of the catch weight on commercial landing size classes of cod from 1987 to 2005 was used. These size classes were divided into immature (<2 kg), mature (>4 kg), and a mixture of mature and immature fish (2–4 kg) and correspond roughly to cod of ages 1 to 2, age 4+, and ages 2 to 4, respectively. The proportion mature in these age groups are <0.05, >0.62, and 0.05–0.62 (ICES 2006).

Comparisons of catch per day and stock biomass

We used a flexible model to describe the relationship between catch rates and stock size:

$$(1) \qquad U = aB^{(1+b)} + c$$

where U is catch rate, B is stock size, and a, b, and c are constants. This model includes increasing catchability at decreasing stock size ($b < 0$ and (or) $c > 0$), decreasing catchability at decreasing stock size ($b > 0$ and (or) $c < 0$), as well as constant catchability ($b = c = 0$) (Fig. 2). As a special case, it includes the power function often used in the literature ($c = 0$, $b \neq 0$) (Bannerot and Austin 1983; Harley et al. 2001). Furthermore, it includes the case where density remains relatively constant in areas unavailable to fishing (e.g., refugia) even when biomass is severely reduced. This leads to catch rates reaching zero at a biomass greater than zero ($c < 0$). Assuming $b = 0$ for simplicity, the biomass of fish in refugia is $-c/a$ as

$$(2) \qquad U = a\left(B + \frac{c}{a}\right) = aB + c$$

Further, the model includes the case where the true amount of fish, B', corresponds to the amount estimated scientifically (B) plus a bias of c/a. The bias term may be either positive or negative, corresponding to scientific under- and over-estimation of biomass, respectively. Underestimation could be the result if a constant amount of fish were unavailable to scientific surveys but remained available to commercial fishing. This could occur if fish residing in areas with large rocks or around wrecks were unavailable to survey trawls but were available to commercial fisheries using stationary gear such as hooks or gill nets. The commercial fishery then catches a constant proportion a of the true biomass per unit effort:

$$(3) \qquad U = aB' = aB + c$$

Note that the change in catch rate caused by the presence of refugia cannot be separated from that caused by overestimation of the stock (both lead to $c < 0$). An intercept smaller than zero should therefore be followed by detailed investigations before drawing conclusions regarding the state of the stock.

Equation 1 has the advantage that the different models of catchability (power function, refuge, and bias models) are nested, and statistical testing is therefore straightforward. To our knowledge, no other studies have included all these models in a formal test. The full model (eq. 1) was used to analyse the relationship between CPUE in both commercial fleets and the high-density area survey by replacing B with either total (T) or spawning stock biomass (S) (both in units of 10^6 kg), depending on which of these exhibited the highest correlation with CPUE. The parameters a, b, and c were estimated by minimizing the residual variation (sum of squares) of the full model.

The residual variation of this model was compared with that of two reduced models: one with $b = 0$ and another with $c = 0$. If these reduced models both provided a significant increase in residual variation (F test), the final model was equivalent to the full model and parameters a, b, and c estimated. However, if setting either $b = 0$ or $c = 0$ led to no significant increase residual variation (F test), the parameter (b or c) with the lowest F value (highest probability of being insignificant) was removed from the model. This reduced model was then compared with a model where $b = c = 0$, and if this reduction did not deteriorate the fit of the model significantly (F test), the final model was reduced to

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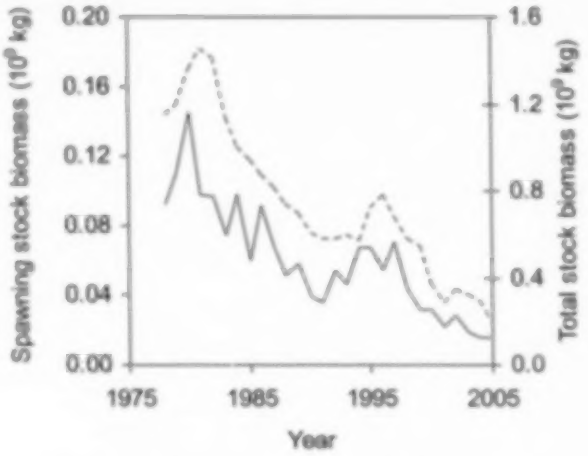
$U = aB$. The procedure is based on the assumption that the error in stock and spawning biomass derived from the assessment is zero or at least negligible compared with that in catch rate. As the assessment is based on total catches, the age composition of catches, and survey catch rates (and hence integrates information from several sources), this assumption appeared reasonable. The parameters of nonlinear models ($b \neq 0$) were estimated using the NLIN procedure in SAS, whereas linear models ($b = 0$) were estimated using the GLM procedure in the same programme (SAS Institute Inc. 2001). Residuals were tested for trends (Pearson correlation with year) and autocorrelation, and their distribution tested for significant differences from a normal distribution (Shapiro–Wilk test).

Unfortunately, restrictive quota regulations may lead to misreporting of effort, catch, area fished, and even vessel size if the catch is brought ashore by another vessel. This may lead to both bias and variation in the estimated catch rates — bias if the catch is not reported at all and variation if the catch is landed by another vessel or reported as being from another area. Hence, both bias and variation may occur in years with restrictive quotas (according to ICES (2006), the years from 2001 and onwards). They will express themselves either as consistent directional deviations from the average relationship between catch rates and stock size or as increases in the variation around the relationship in years with restrictive quotas. Furthermore, technical improvements in fishing power are likely to have occurred over the time span of the study. An increase in fishing power should express itself as an increase in catchability over time. The residuals were therefore examined to determine whether trends or increases in variance occurred.

Distribution of survey catch rates and Danish fishing effort

The spatial distribution of the Danish cod-related fishing effort was compared with the spatial distribution of the survey catch of mature cod per hour through an investigation of the relationship between the centre of gravity of survey catch rates and effort of each fleet in each year and quarter. As catch per day in the Danish fleets consisted of a high proportion of mature fish and was furthermore highly correlated to spawning stock biomass (see Results), the centre of gravity of effort was only compared with the centre of gravity of survey catch rate of mature cod. The centre of gravity of mature cod was estimated from the average catch of mature cod per hour in the IBTS in each statistical rectangle in the first quarter of 1983 to 2006 and the third quarter of 1991 to 2005. The third quarter survey was initiated in 1991 and thus covers only part of the period. The centre of gravity in a given year and quarter was estimated as the average latitude and longitude weighted by the natural log of (1 + the average catch of mature fish (in kg) in each statistical rectangle (sr) (0.5° latitude × 1° longitude)): $\ln(C_{sr} + 1)$. This estimate of the centre was used for survey catches to obtain a homogenous error structure (Rindorf and Lewy 2006). To avoid bias due to differences in survey coverage, only rectangles fished in at least 80% of the years were used. This resulted in 169 and 161 rectangles in the first and third quarter, respectively. The centre of gravity of cod-related fishing effort of a particular fleet in each year and quarter was estimated as the average latitude and longitude weighted by days fished in each statistical rectangle. The Pearson's correlation coefficients between the coordinates (latitude and longitude) of survey and effort centres of gravity were estimated.

Fig. 3. Temporal development in North Sea cod (*Gadus morhua*) total stock biomass (solid line) and spawning stock biomass (broken line).



Results

Development in stock size, effort, and CPUE

Though a slight increase in biomass was observed in the late 1990s, this was followed by decline, and both total and spawning stock biomass has decreased severely over the past 25 years (Fig. 3). Effort has decreased contemporaneously, in particular over the past 10 years (Pearson's correlation coefficients between year (1994–2005) and effort < –0.68 ($P < 0.05$) for all fleets except Danish large trawlers, Fig. 4), and in 2005, the effort of most fleets was less than 25% of the maximum recorded since 1983, the exceptions being Danish small (45%) and large (77%) trawlers. The majority of the reduction of effort can be explained by a reduction in the number of vessels. CPUE series of most fleets show similar temporal patterns (Fig. 4).

Catch composition

More than 80% of the English CPUE consisted of immature cod, whereas the Danish catch generally consisted of a greater proportion of mature than immature cod (Fig. 5). Around 40% of gillnet and seine catches consisted of mature cod and another 40% of a mixture of mature and immature cod, while the proportion of mature and mixed mature and immature in Danish trawl catches was intermediate between these values and those of the English fleets.

Comparisons of CPUE and total stock and spawning stock biomass

As expected from the catch composition, spawning stock biomass showed the highest correlation with catch per day for Danish fleets, whereas total stock biomass showed the highest correlation to English fleets (Table 2). Note that 36

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Fig. 4. Temporal development in yearly effort (*a* and *b*) and yearly average catch per unit effort (CPUE) (*c* and *d*) of the seven fleets examined. Left axis refers to Danish fleets, right axis to English fleets. (*a* and *c*) Danish small trawlers (plus symbols), Danish large trawlers (squares), and English trawlers (triangles). (*b* and *d*) Danish small gillnetters (triangles), Danish large gillnetters (times symbols), Danish seine (squares), and English seine (plus symbols).

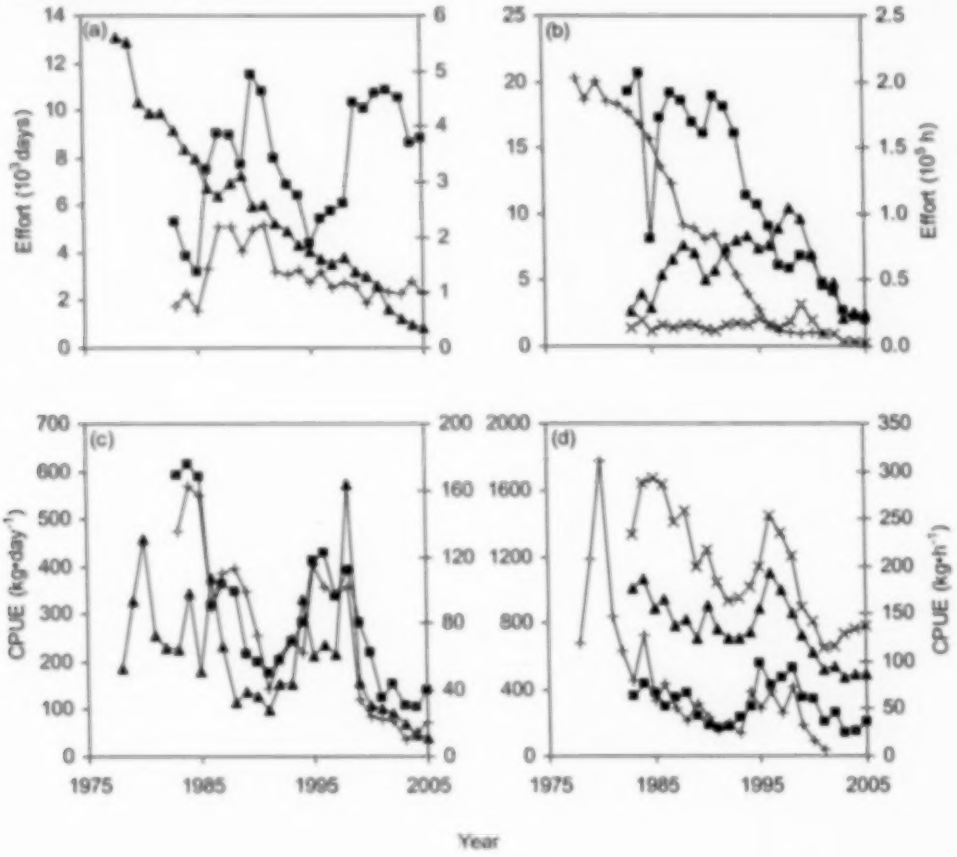
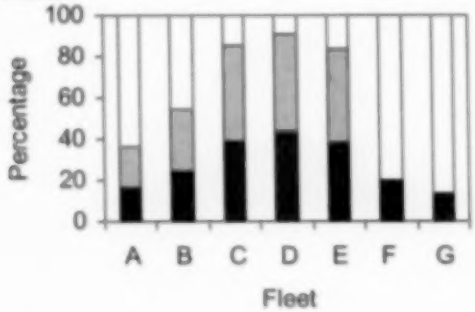


Fig. 5. Cod (*Gadus morhua*) catch composition of the different fleets (yearly average by weight). Mature (black), mixed mature and immature (grey), and immature (open) cod. A, Danish small trawlers; B, Danish large trawlers; C, Danish small gillnetters; D, Danish large gillnetters; E, Danish seine; F, English trawlers; G, English seine.



correlation analyses were performed (not including the IBTS). If the significance level is set to 5%, 5% on average will be termed significant because of type 1 error (detecting significant relationships where none exists). When examining 36 correlations, there is thus a greater than 5% probability of detecting up to four correlations significant at the 5% level (binomial probability > 0.05, $B(36, 0.05)$). At the 1% level, this is decreased to a greater than 5% probability of detecting one or two significant correlations, whereas at a significance level of 0.1%, the probability of detecting one or more significant correlations by type 1 error is 0.035. Therefore, four comparisons should be expected to be significant at the 5% level, two at the 1% level, and none at the 0.1% level by type 1 error alone. In contrast with this, 26 correlations were significant at the 0.1% level for both total stock and spawning biomass, and a further 30 and 32 comparisons were significant at the 1% and 5% level, respectively. Thus, the number of significant relationships greatly exceeds that expected by type 1 error.

Equation 1 was fitted to English CPUE using total stock biomass as the independent variable and to Danish CPUE using spawning stock biomass as the independent variable,

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Table 2. Correlation between catch per unit effort (CPUE) and total stock biomass (*T*), spawning stock biomass (*S*) from stock assessment, and total and mature cod survey catch rate within high-density areas.

		Stock		High-density survey	
Fleet	Quarter	*T*	*S*	Total cod	Mature cod
Danish small trawlers	1	**0.60 (0.0023)**	**0.77 (<0.0001)**	**0.72 (<0.0001)**	**0.53 (0.0089)**
	3	**0.77 (<0.0001)**	**0.84 (<0.0001)**	—	—
Danish large trawlers	1	**0.69 (0.0002)**	**0.80 (<0.0001)**	**0.84 (<0.0001)**	**0.68 (0.0003)**
	3	**0.62 (0.0014)**	**0.81 (<0.0001)**	—	—
English trawlers	All	**0.67 (<0.0001)**	**0.53 (0.0037)**	—	—
Danish small gillnetters	1	**0.83 (<0.0001)**	**0.90 (<0.0001)**	**0.77 (<0.0001)**	**0.67 (0.0005)**
	3	**0.80 (<0.0001)**	**0.86 (<0.0001)**	—	—
Danish large gillnetters	1	**0.73 (<0.0001)**	**0.85 (<0.0001)**	**0.77 (<0.0001)**	**0.74 (<0.0001)**
	3	**0.81 (<0.0001)**	**0.77 (<0.0001)**	—	—
Danish seine	1	0.29 (0.1831)	0.189 (0.3757)	0.34 (0.1168)	0.17 (0.4447)
	3	**0.42 (0.0484)**	**0.42 (0.0489)**	—	—
English seiners	All	**0.91 (<0.0001)**	**0.79 (<0.0001)**	—	—
IBTS	1	**0.88 (<0.0001)**	**0.88 (<0.0001)**	—	—
High-density survey	1	**0.85 (<0.0001)**	**0.77 (<0.0001)**	—	—

Note: Values in parentheses denote probability of no correlation. Significant ($P < 0.05$) correlations are in bold. ITBS, International Bottom Trawl Survey.

as these combinations showed the highest correlation (Table 2). The Danish seiners showed low correlations with both total and spawning stock biomass (Fig. 6, Table 2) and were excluded from further analyses. The parameter *b* was significantly different from 0 in five cases: English seiners, Danish small gillnetters in the first and third quarters, and Danish large gillnetters in the first and third quarters (Table 3). For the English seiners, *b* was larger than zero (the exponent was larger than 1), indicating increased catchability at large stock sizes (Table 3, Fig. 7). In contrast with this, the value of *b* found for Danish gillnetters was negative in all cases (the exponent was less than 1). The intercept was only significantly different from 0 in two cases: Danish small trawlers in the third quarter and English seiners (Table 3). Danish small trawlers showed negative intercepts in both quarters, but only the third quarter value was significantly different from 0, indicating a decrease in catchability at low stock sizes (Fig. 7). The intercept of English seiners was positive; hence, this fleet tended to retain catch rates at a certain minimum level in spite of decreases in stock size corresponding to an increase in catchability at low stock sizes (Fig. 7). In summary, catchability decreased with decreasing spawning stock biomass for Danish small trawlers in the third quarter but increased with decreasing spawning stock biomass for Danish gillnet fleets. Catchability of English seiners decreased with decreasing biomass, though this pattern seemed to reverse at low stock sizes (Fig. 7). However, as the amount of data in the area where catchability supposedly increases was limited, firm conclusions on this would require additional estimates of CPUE at low stock size.

The distribution of the residuals did not differ significantly from a normal distribution for any fleets except for Danish small trawlers and gillnetters in the first quarter, English trawlers, and the high-density surveys catch rates of total and spawning cod ($P = 0.0002$, $P = 0.0111$, $P < 0.0001$, $P = 0.0394$, and $P = 0.0003$, respectively). Only English trawlers exhibited significant trends in the residuals ($P > 0.05$, Table 3, Fig. 8). Thus, there does not appear to have been a general decrease in reported CPUE as a result of reporting only part of the landings but all of the effort. Neither was there any indication of increased catchability due to technical improvements in any fleets except the English trawl fleet. Only Danish small gillnetters in the first quarter exhibited significant autocorrelation of the residuals (correlation = 0.48, $P = 0.0212$).

Comparison between high-density survey catch rates and total and spawning stock biomass

First quarter survey catch rates in high-density areas were highly correlated to both total stock biomass and spawning stock biomass (Fig. 9, Table 2). There was no indication of a nonlinear relationship, as survey catch rates were proportional to the assessment estimates of biomass (Table 3).

Comparison of centres of gravity of survey catches and commercial effort

Latitude of the centre of gravity of survey catches of mature cod increased significantly in both the first and third quarters (Table 4), indicating a northern shift in distribution. Contemporary to the shift in centre of gravity of survey catches, effort of all five Danish fleets moved northeastward in the first quarter (Table 4). The pattern was less clear in the third quarter, as Danish trawlers moved south, while Danish small gillnetters moved north. There was a general trend towards operating in more eastern waters in the third quarter in recent years (Table 4). Effort centres of gravity were closely related to survey centres of gravity for the Danish gillnet and Danish seine fleets in the first quarter, whereas effort centres of gravity of the remaining fleets were only weakly (but positively) related to survey centres of gravity in the same period (Table 4). In contrast with this, the correlation between effort and survey centres of gravity in the third quarter was only significantly positive

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Fig. 6. Relationship between catch per unit effort (CPUE) and (*a* and *b*) stock biomass or (*c*–*g*) spawning stock biomass. Values for Danish fleets refer to the first quarter. (*a*) English trawlers, (*b*) English seiners, (*c*) Danish small trawlers, (*d*) Danish large trawlers, (*e*) Danish small gillnetters, (*f*) Danish large gillnetters, and (*g*) Danish seine. Lines are fitted models for all fleets except Danish seiners, where a linear regression was used (no model was fitted for this fleet).

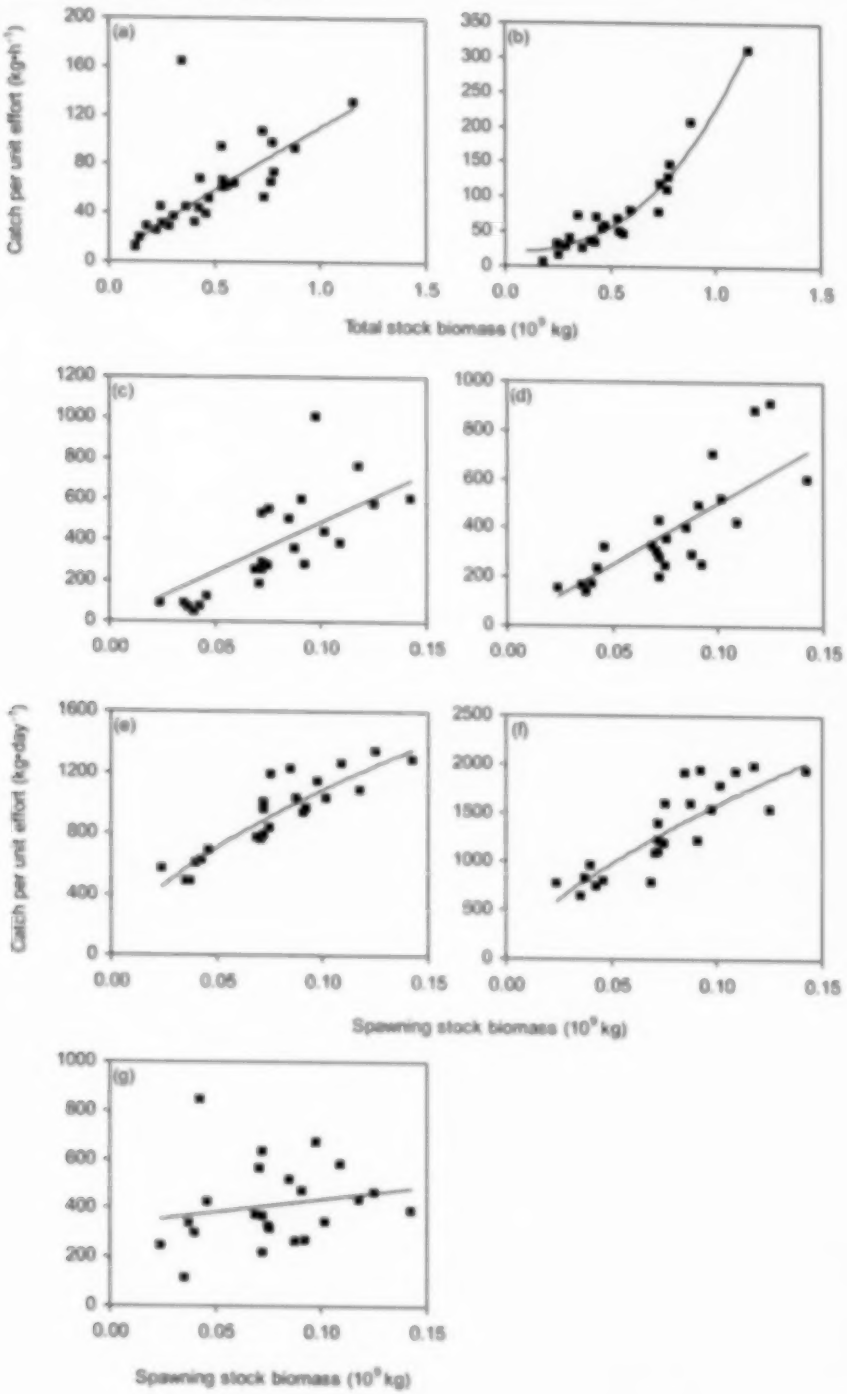

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Table 3. Probability of the parameters b and c being zero and final models (including only significant parameters) of catch rate (U) in either kg·day^{-1} (Danish fleets) or kg·h^{-1} (English fleets and surveys) as a function of total stock (T) or spawning stock (S) biomass (both in 10^6 kg).

Fleet	$P(b = 0 \mid c \neq 0)$	$P(c = 0 \mid b \neq 0)$	$P(b = c = 0)$	Final model	r^2
Quarter 1					
Danish small trawlers	0.5063	0.2734	0.1980[a]	$U = 4.91\ (0.42) \times S$	0.56
Danish large trawlers	0.3060	0.4954	0.2689[b]	$U = 5.05\ (0.33) \times S$	0.64
Danish small gillnetters	0.2803	0.8825	**<0.0001**[b]	$U = 4.55\ (0.81) \times S^{0.62\ (0.07)}$	0.81
Danish large gillnetters	0.5242	0.9724	**0.0124**[b]	$U = 8.26\ (2.12) \times S^{0.71\ (0.10)}$	0.73
Total cod survey catch rate in high density areas	0.5413	0.8036	0.1295[b]	$U = 0.348\ (0.017) \times T$	0.72
Mature cod survey catch rate in high density areas	0.4357	0.5130	0.6177[b]	$U = 0.772\ (0.052) \times S$	0.61
Quarter 3					
Danish small trawlers	0.7541	0.5770	**0.0488**[a]	$U = 4.53\ (0.65) \times S - 0.110\ (0.054)$	0.70
Danish large trawlers	0.1071	0.2624	0.1090[b]	$U = 3.38\ (0.23) \times S$	0.64
Danish small gillnetters	0.6435	0.7493	**0.0004**[b]	$U = 3.61\ (0.77) \times S^{0.62\ (0.09)}$	0.75
Danish large gillnetters	0.7017	0.7069	**0.0009**[b]	$U = 4.27\ (1.14) \times S^{0.56\ (0.11)}$	0.60
Yearly average					
English trawlers	0.5300	0.7296	0.1892[b]	$U = 0.117\ (0.009) \times T$	0.43
English seiners	**<0.0001**	**0.0449**	—	$U = 0.205\ (0.014) \times T^{2.54\ (0.29)} + 0.021\ (0.009)$	0.93

Note: Probabilities significant at the 0.05 level are in bold. Values in parentheses denote standard error of the estimates.

[a] $P(c = 0 \mid b = 0)$.

[b] $P(b = 0 \mid c = 0)$.

for latitude of large trawlers and small gillnetters (Table 4). Hence, there was evidence that effort followed cod distribution in the first quarter, which is the traditional period among fishermen for targeting cod (B.S. Andersen, personal observation), whereas there was only a tendency for effort to follow the latitude of cod distribution in two fleets in the third quarter. Note that as Table 4 examines 44 correlation analyses, five should be significant at the 5% level, two at the 1% level, and none at the 0.1% level by type I error alone (binomial probability > 0.05, $B(44, \alpha)$). However, of the 44 comparisons, 24 were significant at the 5% level, 20 at the 1% level, and 12 at the 0.1% level (Table 4), a much higher number than would be expected by chance.

Discussion

We found no evidence of the presence of refuges, of concentration in high-density areas, or of constant bias in the scientific stock assessment. All fleets except one exhibited a clear relationship between catch rates and either total or spawning stock biomass. Catchability of several fleets changed with stock size, and in two cases, the relationship between catchability and stock size was monotonically decreasing (corresponding to hyperstability of catch rates). However, in spite of this negative relationship, the fleets were unable to compensate for the severe decrease in biomass, and catch rate of all fleets decreased as biomass diminished. Except from a barely significantly positive intercept for English seiners, there was no evidence from any of the fleets of positive intercepts corresponding to scientific underestimation of stock size. Further, only one fleet exhibited a significantly negative intercept corresponding to either fishing outside refuges or scientific overestimation of the stock.

Density in high-density areas was tightly related to stock size in the North Sea, and there was no evidence of nonproportionality. The lack of aggregation rendered the trawl fleets unable to maintain constant high densities, and generally, catchability remained constant in these fleets. Gillnetters often target fish around wrecks and rocks, areas which may support dense fish aggregations (Gregory and Anderson 1997) and which are unavailable to demersal trawl gears. In spite of this, catch rates of gillnetters showed a high degree of agreement with trawl catch rates, indicating that density in trawlable and nontrawlable areas covaried. This agreement may even have increased in later years, as the development of more flexible ground gears has allowed the use of towed gears on bottom substrates previously unavailable to trawlers. The co-occurrence of a northern shift in the spatial distribution of gillnet fishing effort and survey catch rates in the main fishing season also suggests that gillnet catch rates agree with survey catch rates. In contrast, the distribution of the stock in the third quarter inferred from survey catch rates was not generally related to the distribution of effort, indicating either that factors other than cod distribution affect the distribution of effort in this period or that the shorter time period contained less contrast in the centres.

Persistent high densities in some areas in spite of decreases in stock biomass have been found in studies of cod both in the northern Gulf of St. Lawrence and the waters around Newfoundland and Labrador (NAFO areas 3Pn4RS and 2J3KL, respectively) (Rose and Leggett 1991; Rose and Kulka 1999). Presumably as a result of this decoupling of local density and stock size, the catchability of the cod-related trawl fishery increased in both stocks as stock size declined (Rose and Leggett 1991; Rose and Kulka 1999). Why the aggregative behaviour of North Sea cod

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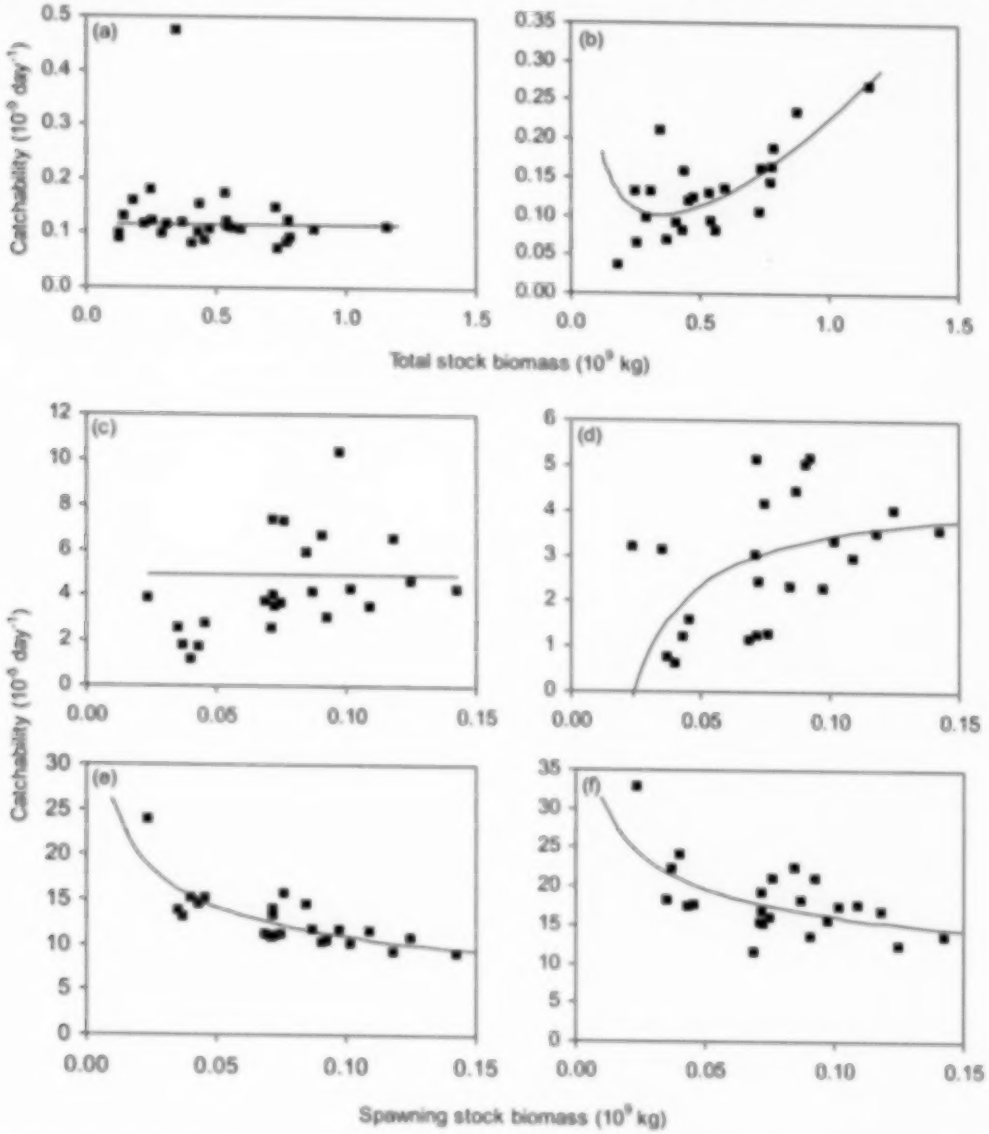
Fig. 7. Relationship between catchability and (*a* and *b*) stock biomass or (*c*–*f*) spawning stock biomass. (*a*) English trawlers, (*b*) English seiners, (*c*) Danish small trawlers in the first quarter, (*d*) Danish small trawlers in the third quarter, (*e*) Danish small gillnetters in the first quarter, and (*f*) Danish large gillnetters in the first quarter. Lines are catchabilities estimated as predicted catch per unit effort (CPUE) from fitted models divided by biomass.



differs from that of cod in other areas remains unknown. Possibly, the North Sea has fewer low-quality habitats, as growth rates in this area have historically been high compared with other areas (Brander 1995). In any event, there was no evidence of aggregation or of increasing trawl catchability at low stock size.

Fleets with a diverse landing composition such as trawlers showed either no or positive relationships between catchability and stock size, whereas specialized cod-directed fleets such as gillnetters showed negative relationships. This corresponds with what is expected from random sampling (trawling) and oversampling of high-density areas resulting from cod being the target species (gillnetters). Contrasting results have been seen in other studies of catchability and stock size of cod, as some authors have found inverse relationships between both commercial and survey catchability and stock size (Winters and Wheeler 1985; Rose and Leggett 1991; Swain et al. 1994), whereas others found no significant relationships, be it positive or negative (Harley et al. 2001, Hanchet et al. 2005). Though other authors have suggested that one common pattern for all fleets targeting a given species should exist (Harley et al. 2001), this seems unlikely, as the tendency for catchability to increase at low stock size is increased by both the aggregative behaviour of

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Fig. 8. Residuals of fitted models (observed catch per unit effort minus model-predicted catch per unit effort). (*a*) English trawlers (solid triagles) and seiners (open triangles); (*b*) Danish small (open triangles) and large (solid triangles) trawlers; (*c*) Danish small (open triangles) and large (solid triangles) gillnetters.

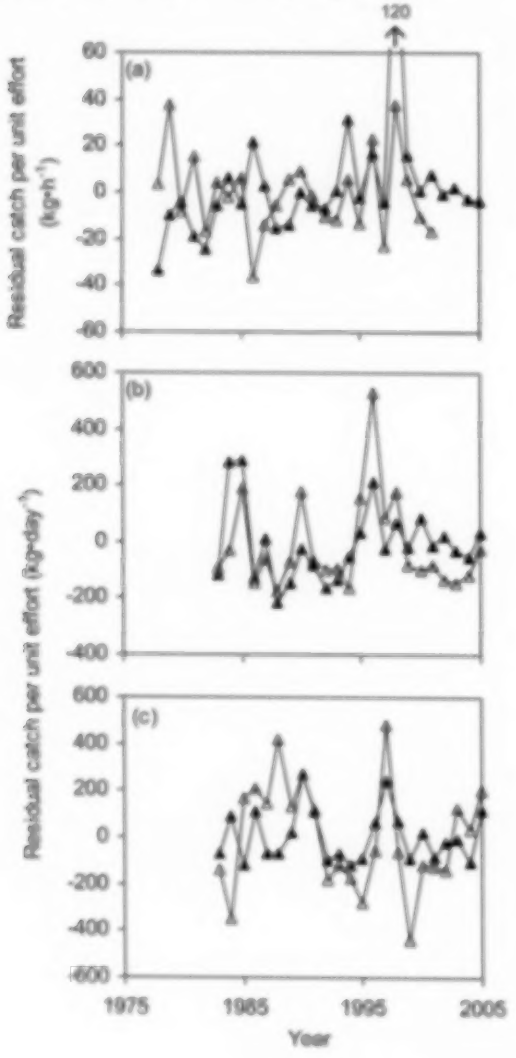
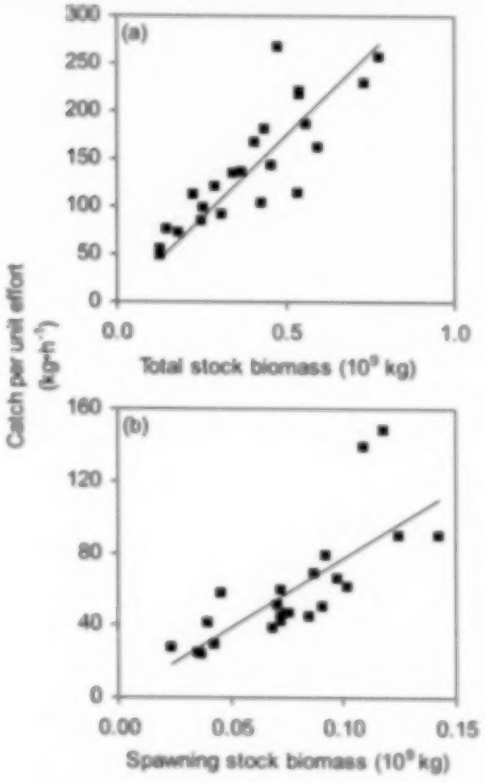


Fig. 9. Relationship between survey catch rate of (*a*) all and (*b*) mature cod in high-density areas and (*a*) total stock and (*b*) spawning stock biomass. Lines are fitted models.



the target species and the degree to which the fishery targets local high-density areas (Paloheimo and Dickie 1964; Hilborn and Walters 1992; Gaertner and Dreyfus-Leon 2004). The difference between the conclusions reached may reflect both differences in the aggregative behaviour of the stocks as well as in the motivation or ability of fishermen to target high-density areas. However, the pattern of constant catchability in mixed-species fisheries and increasing catchability with decreasing stock size in targeted fisheries seen here is likely to be general.

The results obtained here cannot necessarily be generalized to all North Sea fishing fleets. Targeting behaviour and hence catchability is influenced by physical constraints such as vessel type and size, restrictions imposed by management regulation, vessel interactions, information sharing, as well as skipper skills (Gillis et al. 1993; Gillis and Peterman 1998; Gaertner and Dreyfus-Leon 2004), and variation in these decision parameters between fleets and among fishermen within a fleet will create both temporal and spatial diversity in catchability. Though it cannot be generalized to all fisheries, the analysis does, however, present the first thorough multi-fleet analyses of North Sea cod-related fisheries, and the fleets together cover a substantial proportion of the cod landings.

The increased catchability of gillnetters at low stock size could be the result of either an increased aggregation of cod in nontrawlable areas, a correlation between effort allocation and catchability of individual vessels, a gear saturation effect at high stock sizes, or a relationship between catch rates and effort recorded as cod-targeted. Increased aggregation in nontrawlable areas seems unlikely, as there is a fair agreement between gillnet effort distribution and survey catch rate distribution, indicating that the two gear types provide comparable estimates of spatial distribution and therefore most likely also of temporal distribution. A correlation between effort allocation and catchability of individual vessels could occur if individual differences in cod catch rates exists because of, for example, differences in skipper skills and gillnetters with low catch rates switching to other fisheries

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Table 4. Trends (Pearson's correlation coefficient with year) in latitude north (Latitude) and longitude east (Longitude) of effort centre of gravity and correlation between survey and effort centre of gravity.

	Trend				Correlation between survey and effort centre			
	Quarter 1		Quarter 3		Quarter 1		Quarter 3[a]	
Fleet	Latitude	Longitude	Latitude	Longitude	Latitude	Longitude	Latitude	Longitude
Danish small trawlers	**0.60 (0.0026)**	**0.43 (0.0398)**	**–0.66 (0.0006)**	**0.67 (0.0005)**	0.25 (0.2478)	0.02 (0.9234)	–0.34 (0.2218)	–0.02 (0.9566)
Danish large trawlers	**0.48 (0.0217)**	0.41 (0.0539)	0.03 (0.9088)	**0.43 (0.0406)**	0.37 (0.0795)	0.27 (0.2200)	**0.69 (0.0040)**	0.17 (0.5534)
Danish small gillnetters	**0.65 (0.0007)**	**0.97 (<0.0001)**	**0.50 (0.0153)**	**0.88 (<0.0001)**	**0.63 (0.0014)**	**0.59 (0.0030)**	**0.72 (0.0028)**	0.30 (0.2728)
Danish large gillnetters	**0.68 (0.0004)**	**0.78 (<0.0001)**	–0.19 (0.3877)	**0.80 (<0.0001)**	**0.61 (0.0019)**	**0.73 (<0.0001)**	–0.02 (0.9563)	0.51 (0.0522)
Danish seine	**0.77 (<0.0001)**	0.29 (0.1855)	0.05 (0.8109)	–0.11 (0.6021)	**0.74 (<0.0001)**	0.41 (0.0538)	0.49 (0.0611)	0.35 (0.1991)
Survey	**0.73 (<0.0001)**	**0.55 (0.0050)**	**0.76 (0.0011)[a]**	0.23 (0.4103)[a]	—	—	—	—

Note: Values in parentheses denote probability of no correlation. Significant correlations are in bold.

[a]Based on data from 1991 to 2005.

at low stock size. This would lead to an increase in catchability as less efficient vessels shift to other species or leave the fishery. Another explanation for changes in catchability that are unrelated to aggregation of the target species could be gear saturation. This would occur if gill nets become more visible and hence are more easily avoided once some cod have been entangled. To reveal whether this occurs would require detailed studies of density and avoidance behaviour around set nets. Lastly, a relationship between catch rates and effort recorded as cod-targeted could be an artefact caused by the exclusion of gillnet fishing trips where cod was not the main economic species in the landing. Using this method, the gillnet fleet can maintain apparently stable catch rates at low stock size, as only those trips where sufficient cod were caught to obtain the majority of the landing value will be included in the estimate of CPUE. Though this problem seems to arise from the definition of cod-directed fishing effort, using all fishing effort as done for the trawl fleets is not without problems either. In this case, one obtains an overoccurrence of low or zero catches of cod (corresponding to an overestimation of effort), as trawl trips performed in areas uninhabitable by cod and with different gear deployment are included. This problem is likely to increase as cod stock size decreases and more restrictive catch quotas decrease the motivation to target cod. Nevertheless, we believe the definitions used (targeted gillnet fishery and nontargeted trawl and seine fishery) present the least bias among the two alternatives, given that the actual species targeted is unknown.

The low correlation between stock size and catch rates observed in Danish seiners may be caused by several factors. First, over 90% of the Danish seine vessels have been decommissioned during the study period (>500 in 1983 to 47 vessels in 2005), primarily because of a combination of a dramatic decline in the quotas of both cod and other target species and a lack of cod in the southern part of the North Sea, where the majority of the Danish seine fleet traditionally had their home harbour. Most likely, the decommissioning has caused a permanent loss of the least efficient vessels (low catchability vessels) from the fishery. Furthermore, the Danish seine fishery, in contrast with the other Danish fisheries investigated, is primarily a summer fishery, and catch success depends heavily on weather conditions.

The residuals show no evidence of increased catchability (technical creep) or increased misreporting in later years. The fishery has been severely reduced since the implementation of the North Sea cod recovery plan in 2001, and this could have caused both bias and increased variation in reported catch rates within this period. They should have expressed themselves as either consistent directional deviations from the average relationship between catch rates and stock size or as increases in the variation around the relationship in years with restrictive quotas. Nevertheless, there was no tendency for variation in the residuals to increase or exhibit trends in later years. Furthermore, there were only minor changes in the parameters of the models if the years from 2001 onwards were excluded from the estimation procedure (results not shown); hence, the results given here did not appear to be greatly biased by misreporting in later years.

As CPUE of the modelled fleets was highly correlated to

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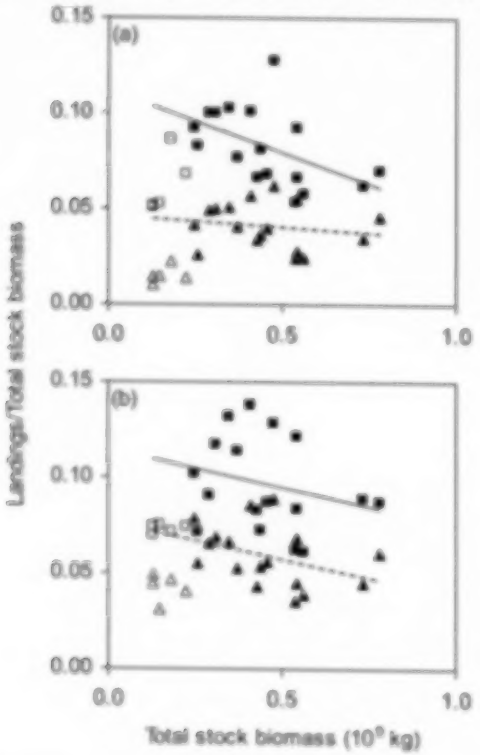
Fig. 10. Relationship between harvest rate (yearly landings / stock biomass) and stock biomass: (*a*) English (triangles) and Scottish (squares) landings; (*b*) Danish (triangles) and other international (squares) landings. Solid and open symbols denote the period before and after the introduction of restrictive quotas in 2001, respectively. Lines are linear regressions for the period before 2001.



stock biomass, the fleets fulfil two of the requirements to an abundance estimate (unbiased residuals and high correlation). These CPUE series may thus be the solution to the need for industry-based series of North Sea cod abundance as a supplement to survey series described by Horwood et al. (2006). However, for these series to be reliable, it must be assured that discard, misreporting of effort and catch, and fishing power does not increase in the future.

A central question from a management point of view is whether any of the fleets examined here would seriously diminish the population if not regulated restrictively. Assuming that the total landings of each fleet provide reliable estimates of catches, this problem is evident by the observed increase in catch divided by total stock biomass as stock biomass decreased up to the year 2000 (Fig. 10). Note that catch of a fleet divided by total stock size is proportional to the partial fishing mortality induced by that fleet if the ratio between average weight of cod in the catch and that in the stock remains constant. The severe decrease in total allowable catch appears to have reduced at least official landings per biomass by about 50%, whereas the regulations prior to this period does not appear to have reduced fishing mortality. Though ICES suggests that the decrease in the observed fishing mortality may partly have been abated by a larger, unspecified mortality in later years (ICES 2006), Horwood et al. (2006) estimated a decrease in cod fishing effort of 37% from 2000 to 2004. The discrepancy between these two estimates cannot be explained at present. However, it is clear that in the absence of the severe reductions in total allowable catch, there would have been a further increase in fishing mortality as stock size decreased, thereby accelerating the decline of the already threatened cod stock.

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Evaluating probability sampling strategies for estimating redd counts: an example with Chinook salmon (*Oncorhynchus tshawytscha*)

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Abstract: Precise, unbiased estimates of population size are an essential tool for fisheries management. For a wide variety of salmonid fishes, redd counts from a sample of reaches are commonly used to monitor annual trends in abundance. Using a 9-year time series of georeferenced censuses of Chinook salmon (*Oncorhynchus tshawytscha*) redds from central Idaho, USA, we evaluated a wide range of common sampling strategies for estimating the total abundance of redds. We evaluated two sampling-unit sizes (200 and 1000 m reaches), three sample proportions (0.05, 0.10, and 0.29), and six sampling strategies (index sampling, simple random sampling, systematic sampling, stratified sampling, adaptive cluster sampling, and a spatially balanced design). We evaluated the strategies based on their accuracy (confidence interval coverage), precision (relative standard error), and cost (based on travel time). Accuracy increased with increasing number of redds, increasing sample size, and smaller sampling units. The total number of redds in the watershed and budgetary constraints influenced which strategies were most precise and effective. For years with very few redds (<0.15 redds·km^{-1}), a stratified sampling strategy and inexpensive strategies were most efficient, whereas for years with more redds (0.15–2.9 redds·km^{-1}), either of two more expensive systematic strategies were most precise.

Résumé : La gestion des pêches requiert comme outils essentiels des estimations précises et non faussées de la taille des populations. Chez une grande diversité de poissons salmonidés, le décompte des frayères dans un échantillon de sections de cours d'eau sert couramment à suivre les tendances annuelles d'abondance. En utilisant une série chronologique de 9 années d'inventaires géoréférencés de frayères de saumons chinook (*Oncorhynchus tshawytscha*) dans le centre de l'Idaho, É.-U., nous testons une gamme étendue de stratégies courantes d'inventaire pour l'estimation de l'abondance totale des frayères. Nous évaluons deux tailles d'unités d'échantillonnage (sections de 200 et de 1000 m), trois proportions échantillonnées (0,05, 0,10 et 0,29), ainsi que six stratégies d'échantillonnage (échantillonnage par indices, échantillonnage aléatoire simple, échantillonnage systématique, échantillonnage stratifié, échantillonnage par groupements adaptatifs et un plan équilibré spatialement). Nous évaluons les stratégies d'après leur exactitude (couverture de l'intervalle de confiance), leur précision (erreur type relative) et leur coût (temps de déplacement). L'exactitude augmente en fonction directe du nombre de frayères et de la taille des échantillons et en fonction inverse de la taille des unités d'échantillonnage. Le nombre total de frayères dans le bassin versant et les contraintes budgétaires déterminent quelles stratégies sont les plus précises et les plus efficaces. Les années avec très peu de frayères (<0,15 frayère·km^{-1}), la stratégie d'échantillonnage stratifié et les stratégies moins chères s'avèrent être les plus efficaces, alors que les années avec plus de frayères (0,15–2,9 frayères·km^{-1}), l'une ou l'autre de deux stratégies systématiques plus coûteuses sont plus précises.

[Traduit par la Rédaction]

Introduction

Chinook salmon (*Oncorhynchus tshawytscha*) populations are important for the economy, recreation, and culture of the Pacific Northwest (Lichatowich 1999). Over the last century, these populations have experienced substantial declines (Lichatowich 1999). Nehlsen et al. (1991) listed 64 Chinook salmon stocks that are at high-to-moderate risk of extinction

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or are of special concern in the region. Ten of these stocks are listed under the United States Endangered Species Act (ESA) (Myers et al. 1998). Hundreds of millions of dollars are spent annually in the Columbia River basin alone to conserve and restore Chinook salmon and other salmonid species ($122 million per year in early 1990s; Lichatowich 1999).

Given the lack of existing experimental design applied to the distribution of management actions, estimation of population status is key to assessing the net impact of habitat degradation, climate change, hatchery practices, harvest, and hydropower. Improving management practices also requires feedback on salmon population response to past management actions (e.g., adaptive management; Bellman 1961; Hilborn 1979; Halbert 1993). Scientific monitoring aims to provide accurate and precise abundance assessments that enable tracking of changes in population attributes for a particular region of interest (Stehman and Overton 1994; Conquest and Ralph 1998; Conquest 2002). Measures of population condition can include both the *size* of the population at a particular time (status) and the change in population size over time (trend). In this paper, we focus on status. For salmonid fishes, these regions of interest may be delimited by the boundaries of evolutionarily significant units (ESU, Waples 1991), hydrological units, watersheds, or other political entities. Censusing every fish in such large areas is prohibitively expensive, even if it were possible. Therefore, a necessary component of monitoring is sampling in a statistically valid and representative manner (Williams 1978). There are numerous sampling strategies, each with a unique set of strengths and weaknesses that can affect the accuracy and precision of parameter estimates. Therefore, determining which strategy is optimal for a given application is important, because it affects the power of the results and project costs (Cochran 1977; Lohr 1999; Larsen et al. 2001).

Most modern monitoring programs, like the US Environmental Protection Agency's (EPA) Environmental Assessment and Monitoring Program (EMAP), are based on probability sampling, which requires that every element, for example, locations or individuals, within the sampling universe possesses a nonzero probability of being included in a given sample (Thompson 1992). Probability designs have several advantages over nonprobability designs. They allow for probability-based inferences about the entire sampling universe, include a measure of uncertainty, and objectively select study elements, thereby removing possible selection bias. Importantly, the specific feature of probability samples that allows for inferences to be extended to the population is the use of randomization for choosing study elements (Fisher 1935).

Historically, monitoring of many salmon populations was based on data from annual commercial harvest of adult fish from the ocean (Lichatowich 1999), but recent monitoring efforts have utilized sport harvest, dam and weir passage counts, stream surveys for juveniles and spawning adults, and counts of nests, often referred to as redds (Myers et al. 1998). In fact, the complex life history of salmon offers many potential indicators of salmon abundance, the merits of each depending on the specific question being addressed.

Redd counts have long been used to monitor salmon populations (Hassemer 1993). Not only do they provide indirect measures of spawner abundance and reproductive effort, but they are relatively easy to observe (especially for species that spawn during low flows) for extended time periods. Despite the ubiquity of redd counts, however, little guidance exists for designing efficient sampling strategies in stream networks. Furthermore, the sampling universe itself has not always been chosen based on best representation of the overall spawning habitat. As a result, estimates of spawning based on redd counts can suffer from a loss of both accuracy and precision because of inefficient sampling designs and less than optimal choice of the sampling universe. Early agency monitoring efforts commonly consisted of establishing index reaches where redds were counted in accessible portions of stream networks with high fish densities (Hassemer 1993). Index reaches are portions of a river or stream where monitoring metrics, such as redd density, are regularly generated as the basis for extrapolating population estimates over a much larger unstudied area. Unfortunately, these reaches are rarely representative of the population as a whole because they were based on a nonprobabilistic sample and can only provide broader inference if untenable assumptions are made (e.g., temporal consistency in spawning distributions). Despite inherent limitations, index sampling remains valuable because of the temporal extent of data at these sites and the ability to examine long-term population dynamics (Isaak et al. 2003).

Our goal was to compare several probability sampling strategies for estimating the total abundance of redds in a large river basin and to demonstrate a process of selecting a sampling strategy. A sampling strategy is a sampling design along with an estimator for the parameter of interest. A unique database consisting of multiple censuses of Chinook salmon redds was used as a baseline for comparison of estimators derived from each strategy. We describe the statistical performance of the different sampling strategies and estimate the economic costs for each design. We conclude with a discussion of the trade-offs associated with sample strategy selection.

Materials and methods

Study site

The Middle Fork Salmon River (MFSR), a National Wild and Scenic River, drains 7330 km^2 of central Idaho (Fig. 1). For most of its length, the river flows through the Frank Church River of No Return Wilderness. The watershed consists of two level 4 USGS hydraulic unit codes (HUCs, ICBEMP 1999) or 126 level 6 HUCs. HUCs are accounting and cataloging units for describing four levels of successively smaller waterways in the United States. From its origin at the confluence of Bear Valley and Marsh Creeks, the MFSR flows north-northeast for 171 km through the Salmon River Mountains and joins the Salmon River 92 km downstream from Salmon, Idaho (Thurow 2000).

Chinook salmon populations in the upper MFSR are composed of wild, indigenous fish referred to as both "spring" and "summer" Chinook salmon based on the timing of adult migration past Bonneville Dam in the lower Columbia River (Matthews and Waples 1991). They are categorized as stream-type Chinook salmon because they rear for at least 1

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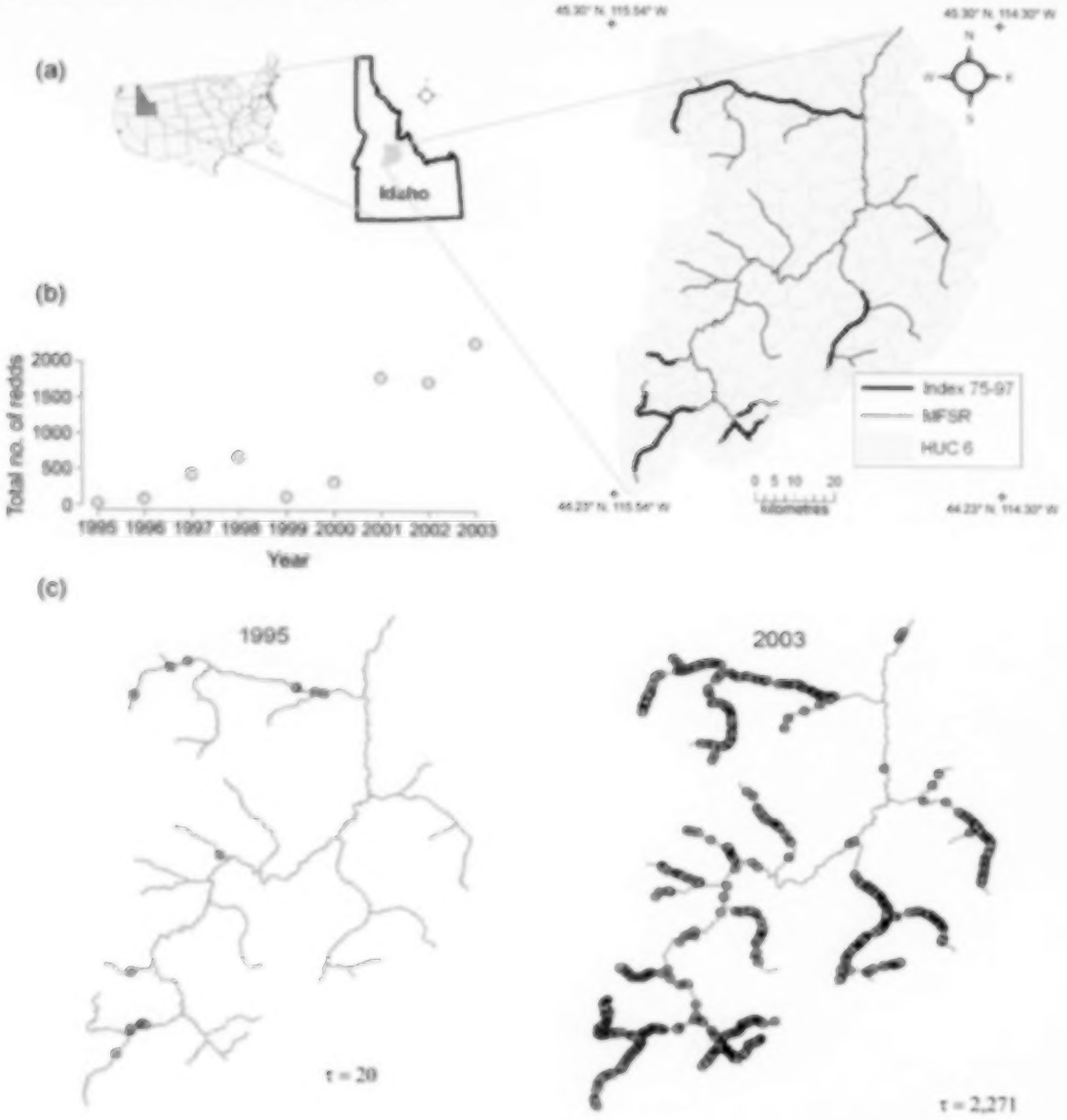
Fig. 1. (*a*) Map of Middle Fork Salmon River (MFSR, Idaho, USA). (*b*) Number of redds for each year. (*c*) Two extreme examples, low- and high-run years, of the census data to be sampled.



year in fresh water (Healey 1991). Adult Chinook salmon enter the MFSR in early summer, migrate toward natal areas in larger tributaries, and stage before spawning. Redd construction usually begins during the last week of July and is completed by mid-September. Females typically deposit eggs in large redds (~3 m^2) constructed in riffle crests or areas with similar hydraulic and substrate characteristics (Healey 1991).

Chinook salmon redd censuses

Since 1995, United States Forest Service (USFS) biologists with the Rocky Mountain Research Station have conducted annual, spatially continuous surveys for Chinook salmon redds within the portion of the MFSR accessible to Chinook salmon. Surveys were conducted using low-altitude helicopter flights at the end of the spawning period (mid-September). Ground observers surveyed stream reaches with closed canopies that were difficult to count aerially (i.e., dense canopy). When a redd was observed, a global positioning system (GPS) was used to geo-reference the location. Both ground and aerial coordinates were differentially corrected and assembled into a geographic information system (GIS) database. For more details, see Isaak and Thurow (2006). We used the data from nine of these surveys (1995

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through 2003) in our analysis; the total number of redds ranged from 20 to 2271 (Fig. 1).

Sampling

The sampling universe was that portion of the stream network surveyed by USFS biologists (Fig. 1). The sampling units were stream segments that were either 200 or 1000 m long. The river network was approximately 680 km of stream and comprised 3400 two-hundred-metre segments and 693 one-thousand-metre segments. Not all of the units were exactly 200 and 1000 m owing to confluences and headwaters. Although a preliminary analysis demonstrated that shorter units result in higher precision, we included the longer units because they were less expensive to sample and were more characteristic of lengths surveyed by agency biologists. Three different percentages of the stream network were sampled: 29%, 10%, and 5% (respectively, n = 1000, 340, and 170 for 200 m segments; n = 204, 69, and 35 for 1000 m segments).

Assumptions and notation

We assumed that redd counts and locations occurred without error, the classical design-based approach to statistical inference (Thompson 1992). Under this assumption, the population values are fixed and the estimators' statistical properties depend solely on the variability caused by the different possible samples. Violation of this assumption would have a minimal effect on our results because all sampling strategies were subject to the same errors.

Let y_i, i = 1,2, …, N, be the population of interest, where y_i is the redd count in river segment i, N = 693 or 3400. Furthermore, let U be the universe of sampling segments, U = {1,2, …, N} and s represent a sample, $s \subseteq U$. Also, define S to be the set of all samples: $s \in S\ \forall\ s \subseteq U$. The parameter of interest is the status, the total number of redds in the watershed, denoted by $\tau = \sum_{i=1}^{N} y_i$. Let $\hat{\tau}$ represent an estimator for τ. The total of the responses in the sample will be denoted by $t = \sum_{i \in s} y_i$. Finally, let $\bar{y} = t/n$ and $\bar{y}_U = \tau/N$ be the sample mean and population mean, respectively.

For design-based inference, the properties of an estimator are based on the sampling strategy rather than an assumed distribution. For example, the expected value of $\hat{\tau}$ is $E[\hat{\tau}] = \sum_{s \in S} p(s)\ \hat{\tau}(s)$, where $s \in S$ indicates the summation over all possible samples, $p(s)$ is the probability that sample s is selected, and $\hat{\tau}(s)$ is the estimate resulting when sample s is selected. The root mean squared error (RMSE) of the estimator $\hat{\tau}$, or standard error if $\hat{\tau}$ is unbiased, is the square root of the variance of its sampling distribution:

$$(1) \qquad \mathrm{SE}(\hat{\tau}) = \sqrt{\mathrm{var}\ (\hat{\tau})} = \sqrt{\sum_{s \in S} p(s)(\hat{\tau}_s - \tau)^2}$$

This standard error is often called the planning standard error because, although it is unknown, it is used to compare different sampling strategies (Lohr 1999). These properties of $\hat{\tau}$ are functions of the entire population and thus are usually unknown to the researcher (see below). The estimated standard error for $\hat{\tau}$, $\widehat{\mathrm{SE}}(\hat{\tau})$, is an estimator for the planning standard error and is a function of the data (see below).

Sampling strategies

Index sampling

Index sampling is a nonrandom sampling design where units are often selected based on stream access and high fish densities. For purposes of this study, we used the 1995–1997 spawning ground index areas established by the Idaho Department of Fish and Game (Elms-Cockrum 1998). These surveys are taken annually at 22 index reaches — some of which have been surveyed for 50 years (Fig. 1). The total length of the index reaches was 198.8 km or about 29.2% of the stream network suitable for Chinook salmon spawning.

To develop status estimators from the nonprobability index sample, we made two assumptions. First, the index reaches covered the entire Chinook salmon spawning grounds, so there were no redds outside this area. By making this assumption, the estimator becomes the simple sum of the sample, $\hat{\tau} = t$. Second, the index sites were representative of the entire network, in which case the resulting estimator inflates the redd count by the fraction of area sampled: $\hat{\tau} = \frac{1}{0.292}\ t = 3.42\ t$.

The two assumptions represent the limits for a family of estimators based on index sampling. We also evaluated estimators intermediate to these that assume index sites represented from 40% to 90% (in increments of 10%) of the total redds in the watershed.

Estimators from index samples do not have a survey design variance associated with them because there is only one possible sample. This is a major limitation of index sampling — no estimate of precision is possible.

Simple random sampling without replacement (SRS)

SRS selects units independently and with equal probability. The estimate for the total number of redds from SRS is $\hat{\tau} = \frac{N}{n}\ t = N\ \bar{y}$, where $\bar{y}$ is the sample mean. This estimator has the variance

$$\mathrm{var}(\hat{\tau}_{\mathrm{SRS}}) = N^2\left(1 - \frac{n}{N}\right)\ \frac{S^2}{n}$$

where $S^2 = \sum_{i=1}^{N}(y_i - \bar{y}_U)^2/(N-1)$ is the population variance and $\bar{y}_U$ is the mean of the response over the universe. The estimator for the planning standard error is

$$(2) \qquad \widehat{\mathrm{SE}}(\hat{\tau}_{\mathrm{SRS}}) = \sqrt{N^2\left(1 - \frac{n}{N}\right)\ \frac{\sum_{i \in s}(y_i - \bar{y})^2}{n-1}}$$

The square of this is unbiased for its respective population variance (Thompson 1992).

Systematic sampling (SYS)

In SYS, every rth unit is selected systematically along a line, for a one-dimensional population, or through space, for a two-dimensional population. An easy way to systematically sample a river network is to connect all tributaries into one line and systematically sample along this line in one dimension. To do this, we calculated the closest integer to N/n, which we denote as K, and chose a random number r between 1 and K, then sampled the rth unit and every Kth

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unit after that. Note that K is the total number of possible systematic samples, where one of these is chosen by the random start. For example, if 5% of the network was sampled, there were only $1/0.05 = 20$ possible systematic samples; thus the standard error could be exactly calculated. However, constructing a single line from a linear network is not uniquely possible, so we had to decide on an ordering for the tributaries. We decided to order the network's tributaries in a random order for every simulation. This added one extra level of randomization to the design. Certainly, if there was good information about the correlation structure between sampling units, the ordering could be optimized for SYS.

The estimator for the number of redds from SYS is $\hat{\tau} = Kt$. The planning variance is intractable in the sense that it is too expensive to calculate, owing to the random ordering of tributaries. Estimating this standard error is in turn complicated by the restrictions imposed by the systematic samples within the tributaries (Bellhouse 1988). The planning variance reflects only cluster-to-cluster variation within tributaries, and since only one cluster is selected for each, an unbiased estimator does not exist. We evaluated three estimators that rely on population assumptions for unbiasedness. The first assumes that the systematic sample is equivalent to an SRS or that the population is in random order:

$$\widehat{\mathrm{SE}}_1(\hat{\tau}_{\mathrm{SYS}}) = \sqrt{N^2\left(1-\frac{n}{N}\right)\frac{\sum_{i\in s}(y_i-\bar{y})^2}{n}} \quad (3)$$

The second, the successive difference estimator, is suggested when the population exhibits a trend (Cochran 1977) within the tributaries:

$$\widehat{\mathrm{SE}}_2(\hat{\tau}_{\mathrm{SYS}}) = \sqrt{N^2\left(1-\frac{n}{N}\right)\frac{\sum_{i\in s}(y_i-y_{i-1})^2}{2n(n-1)}} \quad (4)$$

A final estimator for the variance of the systematic estimator is the neighborhood variance estimator (Stevens and Olsen 2003). This estimator is a weighted average of local estimates of variance, one at each sampled point. The sampled units surrounding each point contribute to each local variance estimator, and their contribution depends on their inclusion probability and the rank (compared with other sampled units in the neighborhood) of their distance from the sampled unit in question. The neighborhoods are not defined in terms of distance but rather by the closest four sampled points (with some adjustment to make the neighborhood function symmetric). The form of the estimator is

$$\widehat{\mathrm{SE}}_3(\hat{\tau}_{\mathrm{SYS}}) = \sqrt{\sum_{i\in s}\sum_{j\in D_i} w_{ij}\left(N\frac{y_j}{n}-\bar{y}_{D_i}\right)^2} \quad (5)$$

Where D_i is the set of sampled units that are the neighbors to unit i, w_{ij} is the weight that decreases as a function of the relative distance of sampled unit j to sampled unit i, and $\bar{y}_{D_i}$ is the weighted average of the units in the neighborhood of unit i.

All three of these standard error estimators are motivated by assumptions about the underlying population autocorrelation structure. They do not specifically estimate the randomization produced by the design nor in particular the effect of the randomizing tributaries to the line along which we sample. The validity of the underlying assumptions on which these estimators are based is unknown, and thus their model-based theoretical properties, such as unbiasedness, are unknown.

Spatially balanced design (GRTS)

The generalized random-tessellation stratified design (GRTS; Stevens and Olsen 1999, 2003) emphasizes spatial balance of the sample in the sense that every sample reflects the spatial balance of the population. It provides better coverage than SRS and more randomness than SYS. For the GRTS design, every unit in the finite population is assigned a random address that was used to order the population randomly, then a systematic design was used to select units along this random ordering as one would do for an SYS sample. The random addresses and the random ordering, however, are closely tied to the spatial location of the units so that the sampled units are spread out in space. The resulting sampling design is similar to a spatially stratified design with one unit selected per stratum; however, the strata are random sets, so the second-order inclusion probabilities are nonzero.

GRTS is an equal probability design, so the estimator for the total is the same as used for SRS, $\hat{\tau} = \frac{N}{n}t = N\bar{y}$. The estimator for the standard error of this estimator is the neighborhood estimator (eq. 5).

Stratified sampling (STR)

In STR, the sampling universe is split up into mutually exclusive but exhaustive strata, and a simple random sample is independently selected from each stratum. There are two reasons to use STR. (*i*) In the case when estimates are required for subsets of the population, STR allows for control over these estimators at the design stage. (*ii*) STR can result in more precise estimators when variability within strata is smaller than variability between strata. We stratified the sample units into two strata based on whether or not they occurred in an index reach. This stratification allows for explicit control over the sampling design within the index reaches and thus control the precision of estimates within the reaches. This advantage is explored further in the Discussion. Furthermore, because the index area is identified as good spawning habitat, we might expect the variance to be smaller within than between the two strata. There are many other possible ways to stratify the MFSR, by tributary, for example, that we did not consider. As in predictive model fitting, we do not want our designs optimized for our training data (the populations we have on the MFSR); rather, we want our results to apply more generally.

We allocated the sample to strata using optimal allocation, which minimizes the standard error of the estimator for the total. Because redd distributions varied through time (Isaak and Thurow 2006), the allocations varied accordingly. Consequently, we calculated the optimal allocation for each year and used the median of these values to allocate the sample to all populations. The resulting allocation was 0.49

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of the sample allocated to the index reaches; the range of the annual optimal allocation was 0.41–0.76.

The estimator for the total number of redds from STR is the sum of the SRS estimators for the strata totals, $\hat{\tau}_{STR} = \sum_{h=1}^{H} \hat{\tau}_h$, where H is the number of strata and $\hat{\tau}_h$ is the SRS estimator for the total within stratum h. Because sampling is independent in each stratum, the variance of this estimator is the sum of the variances of the estimators for each stratum:

$$\text{var}(\hat{\tau}_{STR}) = \sum_{h=1}^{H} \text{var}(\hat{\tau}_h) = \sum_{h=1}^{H} \left(1 - \frac{n_h}{N_h}\right) N_h^2 \frac{S_h^2}{n_h}$$

where the second equality holds under SRS in each stratum, and n_h and N_h are the sample and population sizes for stratum h, respectively. The estimator for this variance is the same function calculated on the sample.

Adaptive cluster sampling (ACS)

ACS begins with SRS. Whenever a sampled unit contains one or more redds, adjacent units are also sampled. If these units also contain one or more redds, their adjacent units are also sampled. Sampling continues until no redds are encountered.

We used the draw-by-draw estimator to estimate the status (Thompson 1992). The population is made up of a series of networks of units, where a network is a set of units that contain redds and would result in the entire network being in the sample if any one of the units is sampled. Let Φ_i denote the network which includes unit i, and let m_i be the number of units in that network. Let ω_i represent the average of the observations in the network, which includes the ith unit of the initial sample, that is, $\omega_i = \frac{1}{m_i} \sum_{j \in \Phi_i} y_j$. The estimator for the total becomes $\hat{\tau}_{ACS} = \frac{N}{n} \sum_{i \in \sigma} \omega_i$, where N and n are still the population and sample size, respectively. The variance of this estimator is

$$\text{var}(\hat{\tau}_{ACS}) = \frac{N(N-n)}{n(N-1)} \sum_{i=1}^{N} (\omega_i - \bar{y})^2$$

The estimate of this variance is the same equation but is calculated on the sample.

For the ACS, the sample size might reflect the size of the original SRS or the size of the final sample that includes elements in the networks. We evaluated both of these approaches; the first was denoted adaptive-n, indicating that the original sample sizes were equal to n above, while the second was denoted adaptive-En, indicating that the original sample sizes were the sample sizes such that the expected final sample sizes were equal to n above. For adaptive-En, the original sample sizes were different for each year and sampling proportion. For example, when 5% of the MFSR was sampled using 200 m units, setting the expected final sample size to 170 resulted in the initial sample sizes of 168, 162, 126, 109, 160, 141, 66, 71, and 41 for redd numbers of 20, 83, 424, 661, 110, 318, 1789, 1730, and 2271, respectively. The resulting final sample sizes varied with number of redds, from 168 to 170 for the fewest (20) and from 41 to 241 for the most (2271). Thompson (1992) describes how to calculate the expected final sample size given a population and an original sample size.

Simulations and statistical evaluation

We evaluated the sampling strategies using Monte Carlo simulations. For each strategy and population, the simulations worked identically; we selected 1000 independent samples from the MFSR segments and calculated $\hat{\tau}$, $\widehat{\text{SE}}(\hat{\tau})$, and cost (see below). The resulting collection of 1000 redd population estimates approximated the sampling distribution of the strategy's estimator for τ so the properties of the estimator could be approximated from this collection of $\hat{\tau}$ values. For example, the standard deviation of this collection approximated the true standard error of the estimator. The simulations were done in the R statistical package (R Foundation for Statistical Computing, Vienna, Austria; code is available from the first author).

The statistical criteria used to compare the strategies were their accuracy and precision. The accuracy of each strategy was evaluated with the empirical coverage of a 95% confidence interval for τ. This empirical probability indicates the fraction of the time that the true total is within the 95% confidence interval around the estimated total and thus is a measure of accuracy. This value should be close to 0.95. Confidence intervals were calculated using the central limit theorem:

$$(6) \qquad \hat{\tau} \pm 1.96 \times \text{SE}(\hat{\tau})$$

There are three elements to this equation; (*i*) a good estimate for the total number of redds (unbiased); (*ii*) a good estimate for the standard error of the estimator for the total (unbiased); and (*iii*) the sampling distribution for the estimator of the total should be well approximated by the normal distribution (the 1.96 constant in eq. 6). Empirical coverage probabilities away from 95% may be due to failure of any of these elements.

Even for accurate strategies, the resulting empirical coverage is unlikely to equal 95% because we are evaluating 1000 replicate samples instead of all possible samples. This is simulation error and it was assessed analytically. If the true coverage probability for a strategy is 0.95, then we would expect 95% of simulated empirical coverages to be within $1.96 \times \text{SE}(\text{cover})$ of 0.95, where cover is the expected nominal coverage, 0.95. This SE was $\sqrt{0.95(1-0.95)/1000} = 0.00689$, so a "hypothesis-test" interval half-width will be approximately 0.014, and we might expect results, when the true coverage probability is 0.95, between 0.936 and 0.964. If the coverage probability falls outside this range, then we conclude that the strategy is not accurate. Precision is defined as the inverse of the standard error; thus, a small variance implies a large precision. We standardized the estimators' planning standard errors (eq. 1) because population sizes (number of redds) varied widely, which because the strategies are unbiased, results in a coefficient of variation (CV):

$$(7) \qquad \text{CV} = \frac{\text{SE}(\hat{\tau})}{\tau}$$

This is the CV for the sampling distribution of the estimator sometimes known as the relative standard error; we shall

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Fig. 2. Location and type of access points (landing strip or trailhead) in the Middle Fork Salmon River (MFSR). Each point along the river system is assigned an access point based on its proximity.

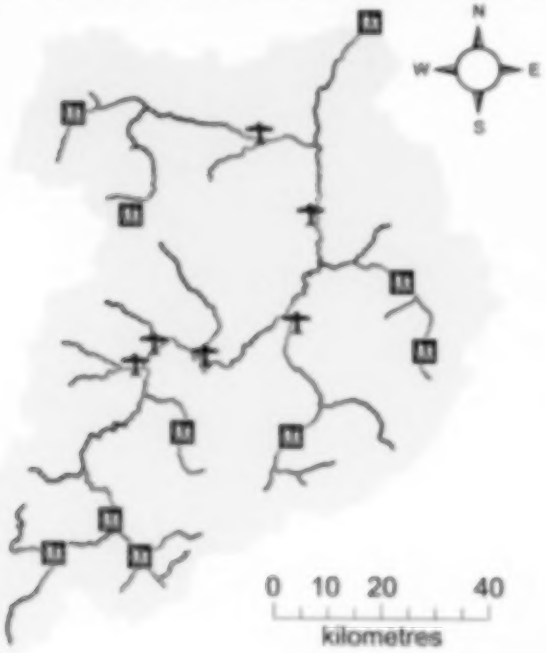
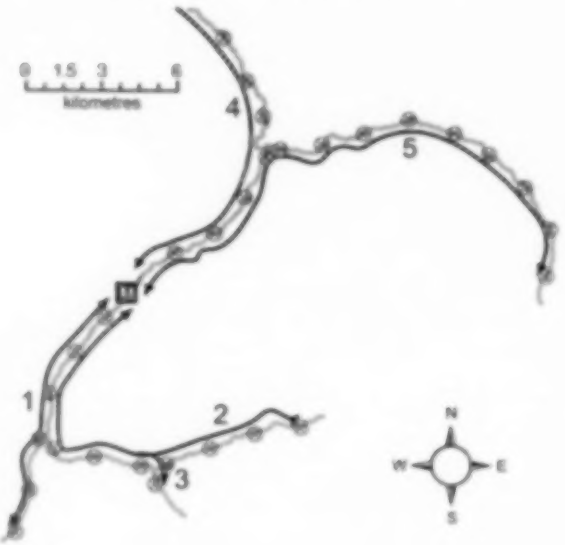


Fig. 3. An example of the cost function. The segments marked with ⊗ are sampled in this systematic random sample. To access these points, the crew makes five trips, marked 1–5, from the access site up each tributary along the black arrows. Notice that trips 2 and 3 are separate distances from the access site. The cost of sampling this region is the total of the crew's travel distance (i.e., the sum of the maximum distance in each of the five river tributary directions).



continue to refer to it as the CV. Small values of CV are desirable. Most of these were calculated analytically and did not suffer from simulation error. For the other cases, we approximated the CV through simulation by calculating the standard deviation of the 1000 estimates for τ. We assessed simulation error here by placing the 1000 replicates into groups of 100. Then we approximated the standard error for $\hat{\tau}$ from each group of 100. The resulting 10 standard errors were used to assess the simulation error for the standard error approximation, and a confidence interval was calculated for the true unknown standard error.

Cost

The MFSR flows primarily through a roadless area with limited vehicle access. Although the censuses that produced the data were collected via aerial surveys, ground-based redd counts are used in many areas, and we wanted to define a cost function that reflects alternative modes of transportation. To begin, we identified 15 access sites (Fig. 2) that signified points past which crews must continue on foot to sample.

To estimate the cost of foot travel, we assigned an access point to each sampling unit and calculated the river distance from the access point to each segment (Fig. 2). We assumed once a crew is dropped off, it can walk up a tributary to the farthest selected site (maximum distance 33 km, median of 10.3 km) and back in one trip counting redds on any additional selected segment on the way. The cost to sample all of the sites along a tributary thus was equivalent to the farthest distance traveled along that tributary, $\max_j\{d_{ij}\}$, where d_{ij} is the distance from sample site j to the access site to which it belongs, i (Fig. 3).

Two other costs were additively included in the cost function: the cost of access and the sampling cost. To estimate the access cost, we assumed that the costs associated with dropping off a crew at any one of the access points are equal. For sampling cost, we assumed it would take five times longer to conduct a redd survey than it would to walk a comparable length of stream. Therefore the complete cost function was

$$C = \sum_{i=1}^{15}(C_i + \max_j\{d_{ij}\}) + 5(l \times n) \quad (8)$$

where the sum is over the 15 access sites, C_i is the cost for access point i, and l is the length of each n sampling segment in kilometres. The cost function has the units kilometres traveled. Because in our case, $C_i = C_j \; \forall \; i, j$, this part of C is ignored.

The costs of the designs were compared, but we also determined which designs were most cost-effective in terms of precision. We evaluated cost and precision together by fixing cost and finding the design that was most precise. Because the index sampling strategy is currently being used, its cost (1254.4 km) was used as a baseline. Because costs varied over the 1000 samples drawn from each design, we chose sample sizes that insured 95% of our samples had costs less than 1254.4 km. Thus, sampling can be accomplished at or under the current index sampling budget with 95% certainty.

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Fig. 4. Simple random sampling with $n = 170\,200$ m units. (*a*) An example of one sample with an enlargement showing the small-scale distribution of sampled segments. (*b*) The approximate sampling distribution for the estimator for status. The mean of these 1000 estimates is 665.4, while the actual number of redds (661) in 1998 is indicated by the vertical line. (*c*) The approximate sampling distribution for the estimator for the standard error. The true standard error for the estimator is 154.66, as indicated by the vertical line. The mean of these 1000 estimators of standard error is 153.6. (*d*) Several examples of confidence intervals; the vertical line indicates the true number of redds (661). Of all the intervals, 939 out of 1000 contain the value 661. Here, iteration number 4 does not contain the truth.

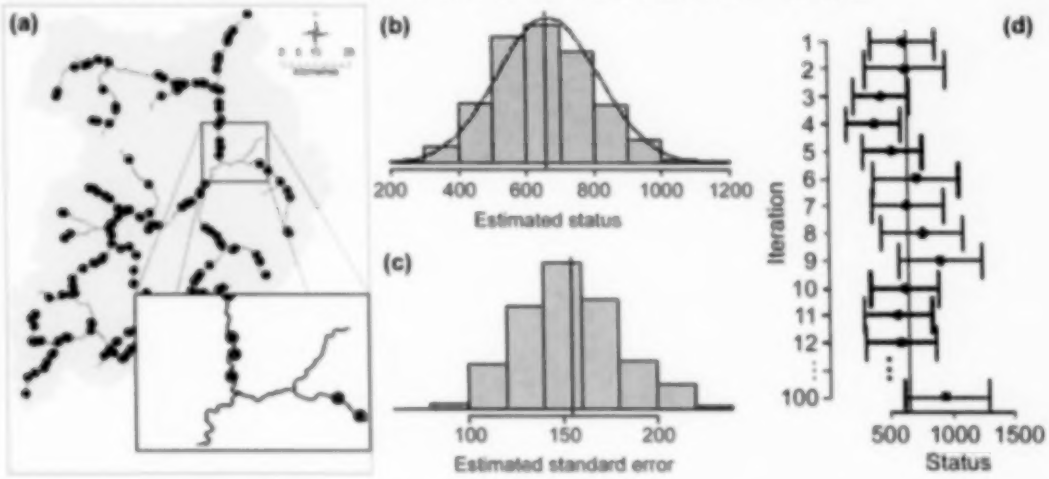
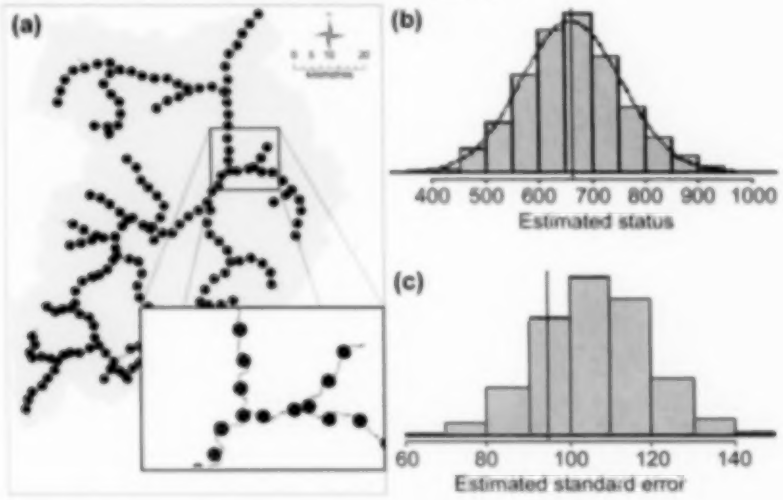


Fig. 5. Systematic sampling with $n = 170\,200$ m units. (*a*) An example of one sample with an enlargement showing the small-scale distribution of sampled segments. (*b*) The approximate sampling distribution for the estimator for status. The mean of these 1000 estimates is 664.35, while the actual number of redds (661) for 1998 is indicated by the vertical line. (*c*) The approximate sampling distribution for the estimator for the standard error that assumes a simple random sample (eq. 2). The true standard error for the estimator is 94.58, as indicated by the vertical line. The mean of these 1000 estimators of standard error is 105.97.



A second method used to evaluate cost and precision was to look at precision per cost, which balances the need for the most informative answer (highest precision) with lowest cost. We defined the standardized precision as the inverse of the CV and measured the precision per cost by

$$(9)\qquad \frac{\text{precision}}{\text{cost}} = \frac{\bar{\tau}}{\text{SE}(\bar{\tau}) \times C}$$

which is in units of 1/(kilometres traveled).

Results

To introduce the analytical protocol and performance measures, we work through two examples that include SRS and SYS for 1998. In both cases, the sampling designs used 200 m units and a 0.1 sampling proportion (Fig. 4). There were $\tau = 661$ redds in the MFSR in 1998 (Fig. 1).

For the SRS (Fig. 4), the average of the 1000 estimates (one from each randomly selected sample) was 658.03, close enough to 661 to suggest that this estimator was accurate

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(unbiased). Since this estimator is unbiased analytically, the difference between 658.03 and 661 was due to simulation error. Furthermore, the sampling distribution for this estimator is approximately normal (Fig. 4*b*). The standard deviation of these 1000 estimates for τ, 107.99, approximated the true standard error of the estimator, which in this case can be calculated exactly as 106.44. The discrepancy between the standard deviation and the true standard error was due to simulation error. The CV, $CV(\hat{\tau}) = 106.44/661 \times 100 = 16.1$, measures the precision of SRS. The average of the 1000 estimates for the standard error was 105.36, suggesting that this estimator is also unbiased (Fig. 4*c*). We demonstrate how for each sample, we can use $\hat{\tau}$ and $\widehat{SE}(\hat{\tau})$ to construct a confidence interval and count how many of these intervals include $\tau = 661$ to determine the empirical coverage probability (Fig. 4*d*). In the SRS case, 924 out of 1000, or 92.4%, include the true value. This value is not within our testing bounds (93.6 to 96.4), indicating that the true coverage was slightly less than 0.95. The reason for this failure is explored later.

For SYS (Fig. 5), $\tau = 661.78$, indicating an unbiased estimator, and the sampling distribution also was approximately normal (Fig. 5*b*). The standard deviation of these 1000 estimates for the total was 94.58 (Fig. 5*c*), resulting in a precision of 14.3. For SYS, we do not calculate the standard error exactly, but depend on the approximation from the simulation. Consequently, this approximation is affected by simulation error. We estimated the magnitude of the simulation error by splitting the 1000 outcomes into 10 groups of 100 each and calculating intervals by using a normal approximation. The 95% interval was 13.9–14.8, and the SYS strategy appeared to be more precise than SRS (14.8 < 16.1).

The average of the 1000 estimates for the standard error, 105.97, was larger than the approximate true standard error of 94.58, indicating a bias in this estimator. In fact, although $\hat{\tau}_{SYS}$ is unbiased, the estimator for the standard error is biased because we used the estimator based on an SRS (eq. 3). This positive bias results in wide confidence intervals and a slightly inflated empirical coverage: 95.9 > 95%. However, this lies within our accuracy bounds (93.6 to 96.4), suggesting that SYS was reasonable.

These two examples indicate the characteristics of accuracy and precision that will be referred to when evaluating the relative performance of the various strategies. We now turn to an evaluation of all the strategies.

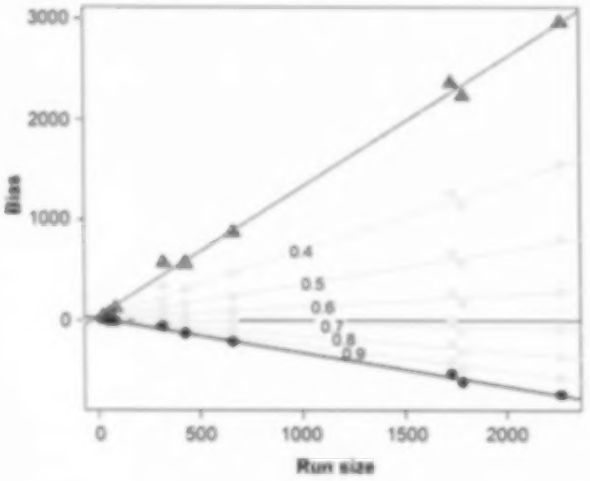
The index strategy

Estimators for the index strategy were biased (Fig. 6). This was not unexpected because the assumptions that had to be made to derive estimates were incorrect. However, approximate estimates could be obtained by assuming that 70% of the redds were in the index reaches regardless of run size. Even with this assumption, however, inaccuracy was still substantial and ranged from 9% (–4.3 redds) in 1999 to 8% (–107.6 redds) in 2001. Because of this large bias and no means of calculating a standard error, additional comparisons between the index strategy and other designs were impossible.

Accuracy

Larger sampling fractions and larger redd numbers resulted in better accuracy (Table 1). Strategies that sampled 200 m segments were more accurate than those sampling 1000 m segments (see bold data vs. shaded cells in Table 1). None of the designs were accurate when redd abundance was low (Table 1). However, as the sampled proportion increased, accuracy improved for intermediate numbers of redds. Only when sampling 29% of the network with 200 m units and during years with large redd numbers could we be confident that nominal 95% confidence intervals are actually 95% (Table 1*c*).

Fig. 6. Actual bias (number of redds) of the estimators from index sampling. The values 0.4–0.9 are the assumed proportion of redds that are in the index reaches (counted) used to construct estimators. All assumptions result in biased estimators, with the bias depending on the run size.



Precision

As redd numbers increased, precision improved for all designs (Tables 2 and 3). Precision also improved as the sampling fraction increased and with 200 m reaches relative to 1000 m reaches (Tables 2 and 3).

The SYS and GRTS designs were most precise, with STR also performing well with lower numbers of redds. SRS and the adaptive designs were generally less precise.

Cost

As expected, designs that select fewer, larger units were less expensive (Figs. 7*a*–7*c*). However, cost differences decreased for larger sampling fractions (Fig. 7*c*). The index design was the least expensive strategy (Fig. 7*c*) when the sampling proportion was large (29%), because the index reaches are clustered near access points; however, the index design was the most expensive for smaller sampling proportions. The least expensive probabilistic strategy was adaptive-En because of its small initial sample sizes; the most expensive was adaptive-n, because of its larger final sample sizes. These two strategies were also the most variable (Figs. 7*a*–7*c*) because the final sample sizes depend on whether the initial SRSs contain any redds and thus were unknown. Cost differences among remaining designs were trivial.

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Table 1. Accuracy as measured by the empirical coverage of the 95% confidence interval.

	Run size								
Strategy	20	83	110	318	424	661	1730	1789	2271
(*a*) Sampling fraction = 0.05 (n = 170).									
SRS	57.5	88.9	88.3	89.2	91.5	92.3	92.8	91.1	93.2
SYS									
1	56.8	90.2	87.5	**95.2**	96.8	**95.7**	**98.2**	97.8	98.1
2	56.8	89.0	87.2	**94.2**	**95.6**	**94.2**	97.8	97.2	97.0
3	56.8	89.0	86.2	93.0	**93.6**	92.0	**96.4**	**95.6**	**95.3**
GRTS	65.7	89.3	83.2	90.2	93.3	**88.4**	93.3	32.1	**95.3**
STR	75.3	88.1	87.9	91.4	91.3	91.1	90.7	89.4	92.7
Adaptive-n	58.4	89.5	92.8	90.5	93.2	**94.7**	**93.6**	93.2	**94.1**
Adaptive-En	56.4	89.2	86.2	91.8	91.8	92.0	92.8	92.8	92.1
(*b*) Sampling fraction = 0.1 (n = 340).									
SRS	81.7	92.1	92.0	92.5	93.0	92.4	**92.9**	92.7	**94.0**
SYS									
1	86.5	90.1	**95.2**	**97.5**	96.6	**95.9**	97.7	**98.8**	**99.5**
2	86.5	89.5	**95.2**	**96.6**	**94.5**	92.7	**96.1**	**97.8**	**97.5**
3	87.3	80.7	92.4	**93.2**	91.4	91.3	92.4	**95.7**	**95.4**
GRTS	86.7	86.4	89.1	91.9	**96.3**	**95.2**	**94.0**	**95.7**	**94.0**
STR	82.8	91.0	91.7	92.9	**94.6**	92.9	93.3	91.9	**94.6**
Adaptive-n	82.9	92.6	92.0	93.1	**94.0**	**95.0**	**92.5**	**92.6**	**95.6**
Adaptive-En	84.2	91.9	86.2	92.2	92.7	**95.1**	**94.3**	93.5	**95.5**
(*c*) Sampling fraction = 0.29 (n = 1000).									
SRS	84.8	**94.6**	92.6	**95.3**	**94.4**	**94.5**	**94.9**	**94.3**	**96.2**
SYS									
1	**96.1**	**95.8**	99.7	97.9	96.0	96.4	97.8	99.9	99.7
2	**96.1**	**95.3**	99.1	**95.2**	91.9	91.5	92.6	98.3	97.6
3	98.4	**95.9**	99.5	96.9	94.3	94.7	96.0	99.5	99.2
GRTS	91.4	92.8	**93.9**	**95.5**	**96.1**	**96.2**	**94.2**	**95.1**	97.8
STR	92.4	**95.1**	92.9	**94.6**	92.6	**93.3**	93.2	93.4	93.0
Adaptive-n	87.9	**94.2**	93.4	**94.4**	**95.0**	**93.8**	**95.3**	**94.8**	**95.8**
Adaptive-En	92.6	**94.3**	**94.3**	**94.3**	**94.2**	**96.0**	**95.4**	**95.1**	**94.2**

Note: The data indicate the approximate accuracies for the strategies when sampling 200 m units. A strategy is accurate if its empirical coverage is between 93.6% and 96.4%. Accurate strategies are indicated in bold for 200 m units or shaded for 1000 m units (values not given). SRS, simple random sampling; SYS, systematic sampling; GRTS, spatially balanced design; STR, stratified sampling; Adaptive-n, adaptive cluster sampling when n = the original sample size; Adaptive-En, adaptive cluster sampling when n = the expected final sample size. The three rows for SYS refer to the three estimators for the standard error: 1 = assuming simple random sampling (eq. 2); 2 = successive difference estimator (eq. 3); and 3 = neighborhood estimator (eq. 4).

Precision per unit cost

When costs were held constant, the general trend was for inexpensive designs, such as STR, to have larger sample sizes. As a consequence of more samples, these inexpensive designs were more precise when there were small numbers of redds. Conversely, the more expensive strategies, such as SYS and GRTS, were most precise during large runs, when sparsely distributed redds was less of an issue (Table 4).

Precision per cost also demonstrated that the choice of an optimal design and sample unit size depended on the sample size and run size. For small sample proportions (5%), the inexpensive, larger sampling units (1000 m) provided better value than the smaller 200 m units (Table 5*a*). In this case, the STR strategy was best for small runs and the GRTS strategy was best for large runs (Table 5*a*). However, for the intermediate sample size (10% sampling fraction), during small run years, sampling 1000 m units was most cost effective, while for large-run years, the more expensive SYS design with 200 m units was most cost effective (Table 5*b*). Finally, for large samples, the expensive but precise SYS strategy with 200 m units was most cost effective (Table 5*c*).

Discussion

We examined the performance of different redd sampling strategies for a large river network. Our results illustrate design tradeoffs and can provide guidance for selecting optimal monitoring strategies.

We did not exhaust the set of possible probability sampling strategies that can be used to count redds. We concentrated on standard designs and designs that have been suggested in the literature. Our goal was not to optimize a strategy for the MFSR, but rather to suggest designs that can be used more generally. Likewise, the estimators we considered were also standard, and there may be ways to

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Table 2. Precision for strategies using 200 m units as measured by coefficient of variation × 100 (eq. 7).

	Run size								
Strategy	20	83	110	318	424	661	1730	1789	2271
(*a*) Sampling fraction = 0.05 (*n* = 170).									
SRS	110.9	52.8	50.8	33.9	28.3	23.4	20.2	20.8	18.4
SYS*	107.6	51.9	50.6	26.8	22.9	20.5	14.8	15.0	13.5
GRTS*	95.8	50.1	49.4	34.0	25.2	23.2	16.7	17.7	13.7
STR	86.7	45.8	42.4	27.3	25.3	20.9	17.9	19.3	15.8
Adaptive-n	110.9	52.0	48.7	32.6	26.5	21.6	17.1	17.6	15.5
Adaptive-En	111.6	53.3	50.3	36.0	30.9	27.2	26.8	28.7	32.3
(*b*) Sampling fraction = 0.1 (*n* = 340).									
SRS	76.3	36.3	35.0	23.3	19.5	16.1	13.8	14.3	12.6
SYS*	69.2	39.1	28.1	16.7	16.1	14.3	10.5	10.2	9.1
GRTS*	65.3	35.1	34.6	22.0	15.2	13.3	11.4	11.0	10.0
STR	58.6	31.3	28.9	18.6	17.3	14.3	12.2	13.3	10.8
Adaptive-n	76.3	35.8	33.5	22.5	18.2	14.8	11.7	12.1	10.7
Adaptive-En	76.7	36.7	33.5	24.7	21.1	18.4	17.9	19.0	19.7
(*c*) Sampling fraction = 0.29 (*n* = 1000).									
SRS	39.4	18.8	18.1	12.1	10.1	8.3	7.1	7.4	6.5
SYS*	23.5	16.4	11.7	9.6	9.3	7.6	5.8	4.5	4.0
GRTS*	39.9	19.1	17.8	10.4	8.0	6.2	5.9	5.6	4.3
STR	27.3	15.4	14.0	8.9	8.7	7.2	6.2	6.8	5.4
Adaptive-n	39.4	18.5	17.3	11.6	9.4	7.7	6.1	6.3	5.5
Adaptive-En	39.6	18.9	17.8	12.5	10.6	9.1	8.0	8.8	8.2

Note: The most precise strategies for each run size (column) are shaded; when more than one strategy is highlighted within a column, the difference in precision is unclear because of simulation error. SRS, simple random sampling; SYS, systematic sampling; GRTS, spatially balanced design; STR, stratified sampling; Adaptive-n, adaptive cluster sampling when *n* = the original sample size; Adaptive-En, adaptive cluster sampling when *n* = the expected final sample size.

*Precision is evaluated through simulation.

improve them that we did not consider. In particular, we did not consider any modern variance estimators, for example, the bootstrap may result in more accurate estimators.

Given that the ecological processes that determine the redd distributions we observed are likely to be similar in other locations, our results will be fairly robust. However, given that we do not know this to be true, the relative performance of these sampling designs may not be similar in all other cases.

Poor accuracies

It may be confusing that theoretically accurate strategies, those with unbiased estimators and unbiased estimators of variance, SRS and STR for example, were not consistently accurate. There are two reasons for this failure: small counts and the sensitivity of the normal approximation in the confidence intervals (eq. 6).

During small runs, many of the samples contained zero redds. In these cases, the estimate of the standard error and the confidence interval were zero (Fig. 8*a*). When this occurred, our confidence intervals did not contain the true value and the accuracy suffered. In 1995 (20 redds), for the 0.05 sampling fraction and 200 m units, 437 of the 1000 SRSs had zero redds. These zeros cause a loss of precision during small runs.

The surprising performances of all the designs, but the adaptive sampling design in particular, during small run sizes illustrate an interesting dynamic where the spatial structure of the sampling units interacts with the spatial structure of the sampled populations. In this case, the interaction results in numerous samples that have no redds. This poses a problem for estimation of clustered and rare populations and illuminates the need for a solution. One possible solution is to recruit a design-based likelihood estimator when a large number of zero redd counts are observed (Nicholson and Barry 1995). One could estimate the likelihood of observing zero redds in a sample given a range of very small population sizes pre hoc, and then identify the 95% confidence intervals for the estimated likelihood. Such design-based estimators could explicitly prevent estimating zero redds (Kincaid 1997). Solutions to this interesting design problem may become increasingly important for those designing monitoring for other more rare or endangered populations.

For the larger runs, there were few zeros; however, the accuracies still consistently deviated from nominal. In this case, there appears to be a failure in the normal approximation. Although histograms of the estimates appear normal on inspection, the estimator for the total and the estimator for its standard error were highly correlated (Fig. 8*b*). This correlation existed for most of the strategies regardless of the number of redds or the sample size. For SRS with 200 m units and 0.1 sampling proportion, these correlations ranged from 0.77 to 0.93. This positive correlation would be absent in data that is normally distributed and where the variance

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Table 3. Precision for strategies using 1000 m units as measured by coefficient of variation × 100 (eq. 7).

Strategy	Run size								
	20	83	110	318	424	661	1730	1789	2271
(*a*) Sampling fraction = 0.05 (n = 35).									
SRS	129.1	63.8	66.8	50.8	43.0	35.4	33.8	35.8	32.2
SYS*	115.6	59.6	62.8	42.9	39.3	29.6	27.8	31.9	25.0
GRTS*	65.4	47.4	172.0	21.3	35.6	24.5	24.0	25.2	18.2
STR	94.4	49.9	49.6	36.0	35.2	29.3	27.4	30.3	25.4
Adaptive-n	127.7	58.5	59.7	44.5	38.1	29.8	25.0	24.4	23.5
Adaptive-En	131.8	65.7	69.7	62.8	61.3	56.9	61.6	66.0	63.7
(*b*) Sampling fraction = 0.1 (n = 69).									
SRS	85.6	44.3	46.3	35.2	29.8	24.6	23.4	24.9	22.3
SYS*	81.7	38.9	38.0	23.6	22.2	19.6	16.9	19.1	17.0
GRTS*	38.9	29.9	47.8	21.6	23.8	18.4	17.0	15.4	14.9
STR	64.4	34.2	33.9	24.6	24.2	20.2	18.9	20.9	17.5
Adaptive-n	88.6	40.6	41.4	30.9	26.5	20.7	17.3	16.9	16.3
Adaptive-En	91.6	45.5	48.3	42.6	42.1	38.9	41.6	44.3	42.8
(*c*) Sampling fraction = 0.29 (n = 204).									
SRS	46.1	22.8	23.8	18.1	15.4	12.6	12.1	12.8	11.5
SYS*	50.1	21.3	16.3	12.1	10.2	7.6	7.3	6.7	6.8
GRTS*	40.2	19.7	21.1	13.4	13.2	10.6	11.0	8.4	8.6
STR	28.5	16.1	15.5	11.2	11.9	10.1	9.4	10.5	8.6
Adaptive-n	45.6	20.9	21.3	15.9	13.6	10.7	8.9	8.7	8.4
Adaptive-En	46.8	23.2	24.3	20.8	19.7	18.3	19.8	20.9	21.7

Note: The most precise strategies for each run size (column) are shaded; when more than one strategy is highlighted within a column, the difference in precision is unclear because of simulation error. SRS, simple random sampling; SYS, systematic sampling; GRTS, spatially balanced design; STR, stratified sampling; Adaptive-n, adaptive cluster sampling when n = the original sample size; Adaptive-En, adaptive cluster sampling when n = the expected final sample size.

*Precision was evaluated through simulation.

and the mean are independent. However, in the MFSR redd data, when one underestimates the number of redds, one also underestimates the variance of the estimator, resulting in a loss of accuracy. This effect was most certainly due to the fact that we were analyzing counts that are bounded by zero, making estimators based on the central limit theorem slow to converge in this way (one needs large counts or very large samples). Various transformations of the data were unable to eliminate this consequence of zero counts.

Accuracy of the SYS strategy

The trends in accuracy for the SYS design differed from the other strategies. This strategy was more accurate at intermediate run sizes than at large run sizes, and its confidence intervals appeared too wide and contained the true value too often, resulting in empirical levels above 95%. This situation results because the estimators for the standard error were biased high (Fig. 9); thus, this overestimated estimator counteracts the zero and mean–variance correlation problems discussed earlier. The interaction seemed to work in our favor for the intermediate run sizes, but the overestimated variance dominated for larger run sizes (accuracies >95%), while the zero problem dominated for the smaller run sizes (accuracies <95%).

The reasons for the failure of these estimators were not intuitive. Systematic designs perform well because their implicit spatial balance avoids bad samples that occur under many of the other designs — bad samples being those that have all the sampled locations occurring in some small or limited portion of the watershed. These bad samples with poor spatial balance across the entire sampled universe are possible in designs like SRS. Since the naïve standard error estimator based on SRS (eq. 3) assumes that every sample is possible, including these bad samples, it tends to overestimate the standard error of the systematic samples and is therefore biased for these designs. The properties of the neighborhood estimator, on the other hand, vary depending on the sampling proportion and the stochastic nature of the population response. These factors interact because the neighborhoods are not defined by the responses of points within some fixed radius in space, but rather the population responses measured at the four closest points. For high sampling fractions, the estimator for the variance will depend on an average of sampled points very close together, which one might expect to be relatively well correlated, all else being equal. However, when sampling a small proportion of the watershed, the neighborhood is made up of observations farther apart and is therefore expected to be less correlated. Additionally, as the response becomes increasingly stochastic, spatial correlation will fall faster for a given increase in neighborhood size, and as a result the standard error estimator will increase even more quickly. Furthermore, Stevens and Olsen (2003) report that if the population has no spatial structure, the local estimates of variance estimate the plan-

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Table 2. Precision for strategies using 200 m units as measured by coefficient of variation × 100 (eq. 7).

	Run size								
Strategy	20	83	110	318	424	661	1730	1789	2271
(*a*) Sampling fraction = 0.05 (n = 170).									
SRS	110.9	52.8	50.8	33.9	28.3	23.4	20.2	20.8	18.4
SYS*	107.6	51.9	50.6	**26.8**	**22.9**	**20.5**	**14.8**	**15.0**	**13.5**
GRTS*	**95.8**	50.1	49.4	34.0	**25.2**	23.2	16.7	17.7	**13.7**
STR	**86.7**	**45.8**	**42.4**	**27.3**	25.3	**20.9**	17.9	19.3	15.8
Adaptive-n	110.9	52.0	48.7	32.6	26.5	21.6	17.1	17.6	15.5
Adaptive-En	111.6	53.3	50.3	36.0	30.9	27.2	26.8	28.7	32.3
(*b*) Sampling fraction = 0.1 (n = 340).									
SRS	76.3	36.3	35.0	23.3	19.5	16.1	13.8	14.3	12.6
SYS*	69.2	**39.1**	**28.1**	**16.7**	**16.1**	**14.3**	**10.5**	**10.2**	**9.1**
GRTS*	**65.3**	**35.1**	34.6	22.0	**15.2**	**13.3**	**11.4**	**11.0**	10.0
STR	**58.6**	31.3	**28.9**	18.6	17.3	14.3	12.2	13.3	10.8
Adaptive-n	76.3	35.8	33.5	22.5	18.2	14.8	11.7	12.1	10.7
Adaptive-En	76.7	36.7	33.5	24.7	21.1	18.4	17.9	19.0	19.7
(*c*) Sampling fraction = 0.29 (n = 1000).									
SRS	39.4	18.8	18.1	12.1	10.1	8.3	7.1	7.4	6.5
SYS*	23.5	16.4	**11.7**	9.6	9.3	7.6	**5.8**	**4.5**	**4.0**
GRTS*	39.9	19.1	17.8	10.4	**8.0**	**6.2**	**5.9**	5.6	**4.3**
STR	**27.3**	**15.4**	14.0	**8.9**	8.7	7.2	6.2	6.8	5.4
Adaptive-n	39.4	18.5	17.3	11.6	9.4	7.7	6.1	6.3	5.5
Adaptive-En	39.6	18.9	17.8	12.5	10.6	9.1	8.0	8.8	8.2

Note: The most precise strategies for each run size (column) are shaded; when more than one strategy is highlighted within a column, the difference in precision is unclear because of simulation error. SRS, simple random sampling; SYS, systematic sampling; GRTS, spatially balanced design; STR, stratified sampling; Adaptive-n, adaptive cluster sampling when n = the original sample size; Adaptive-En, adaptive cluster sampling when n = the expected final sample size.

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improve them that we did not consider. In particular, we did not consider any modern variance estimators, for example, the bootstrap may result in more accurate estimators.

Given that the ecological processes that determine the redd distributions we observed are likely to be similar in other locations, our results will be fairly robust. However, given that we do not know this to be true, the relative performance of these sampling designs may not be similar in all other cases.

Poor accuracies

It may be confusing that theoretically accurate strategies, those with unbiased estimators and unbiased estimators of variance, SRS and STR for example, were not consistently accurate. There are two reasons for this failure: small counts and the sensitivity of the normal approximation in the confidence intervals (eq. 6).

During small runs, many of the samples contained zero redds. In these cases, the estimate of the standard error and the confidence interval were zero (Fig. 8*a*). When this occurred, our confidence intervals did not contain the true value and the accuracy suffered. In 1995 (20 redds), for the 0.05 sampling fraction and 200 m units, 437 of the 1000 SRSs had zero redds. These zeros cause a loss of precision during small runs.

The surprising performances of all the designs, but the adaptive sampling design in particular, during small run sizes illustrate an interesting dynamic where the spatial structure of the sampling units interacts with the spatial structure of the sampled populations. In this case, the interaction results in numerous samples that have no redds. This poses a problem for estimation of clustered and rare populations and illuminates the need for a solution. One possible solution is to recruit a design-based likelihood estimator when a large number of zero redd counts are observed (Nicholson and Barry 1995). One could estimate the likelihood of observing zero redds in a sample given a range of very small population sizes pre hoc, and then identify the 95% confidence intervals for the estimated likelihood. Such design-based estimators could explicitly prevent estimating zero redds (Kincaid 1997). Solutions to this interesting design problem may become increasingly important for those designing monitoring for other more rare or endangered populations.

For the larger runs, there were few zeros; however, the accuracies still consistently deviated from nominal. In this case, there appears to be a failure in the normal approximation. Although histograms of the estimates appear normal on inspection, the estimator for the total and the estimator for its standard error were highly correlated (Fig. 8*b*). This correlation existed for most of the strategies regardless of the number of redds or the sample size. For SRS with 200 m units and 0.1 sampling proportion, these correlations ranged from 0.77 to 0.93. This positive correlation would be absent in data that is normally distributed and where the variance

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Table 3. Precision for strategies using 1000 m units as measured by coefficient of variation × 100 (eq. 7).

	Run size								
Strategy	20	83	110	318	424	661	1730	1789	2271
(*a*) Sampling fraction = 0.05 (n = 35).									
SRS	129.1	63.8	66.8	50.8	43.0	35.4	33.8	35.8	32.2
SYS*	115.6	59.6	62.8	42.9	39.3	29.6	27.8	31.9	25.0
GRTS*	65.4	47.4	172.0	21.3	35.6	24.5	24.0	25.2	18.2
STR	94.4	49.9	49.6	36.0	35.2	29.3	27.4	30.3	25.4
Adaptive-n	127.7	58.5	59.7	44.5	38.1	29.8	25.0	24.4	23.5
Adaptive-En	131.8	65.7	69.7	62.8	61.3	56.9	61.6	66.0	63.7
(*b*) Sampling fraction = 0.1 (n = 69).									
SRS	85.6	44.3	46.3	35.2	29.8	24.6	23.4	24.9	22.3
SYS*	81.7	38.9	38.0	23.6	22.2	19.6	16.9	19.1	17.0
GRTS*	38.9	29.9	47.8	21.6	23.8	18.4	17.0	15.4	14.9
STR	64.4	34.2	33.9	24.6	24.2	20.2	18.9	20.9	17.5
Adaptive-n	88.6	40.6	41.4	30.9	26.5	20.7	17.3	16.9	16.3
Adaptive-En	91.6	45.5	48.3	42.6	42.1	38.9	41.6	44.3	42.8
(*c*) Sampling fraction = 0.29 (n = 204).									
SRS	46.1	22.8	23.8	18.1	15.4	12.6	12.1	12.8	11.5
SYS*	50.1	21.3	16.3	12.1	10.2	7.6	7.3	6.7	6.8
GRTS*	40.2	19.7	21.1	13.4	13.2	10.6	11.0	8.4	8.6
STR	28.5	16.1	15.5	11.2	11.9	10.1	9.4	10.5	8.6
Adaptive-n	45.6	20.9	21.3	15.9	13.6	10.7	8.9	8.7	8.4
Adaptive-En	46.8	23.2	24.3	20.8	19.7	18.3	19.8	20.9	21.7

Note: The most precise strategies for each run size (column) are shaded; when more than one strategy is highlighted within a column, the difference in precision is unclear because of simulation error. SRS, simple random sampling; SYS, systematic sampling; GRTS, spatially balanced design; STR, stratified sampling; Adaptive-n, adaptive cluster sampling when n = the original sample size; Adaptive-En, adaptive cluster sampling when n = the expected final sample size.

*Precision was evaluated through simulation.

and the mean are independent. However, in the MFSR redd data, when one underestimates the number of redds, one also underestimates the variance of the estimator, resulting in a loss of accuracy. This effect was most certainly due to the fact that we were analyzing counts that are bounded by zero, making estimators based on the central limit theorem slow to converge in this way (one needs large counts or very large samples). Various transformations of the data were unable to eliminate this consequence of zero counts.

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The trends in accuracy for the SYS design differed from the other strategies. This strategy was more accurate at intermediate run sizes than at large run sizes, and its confidence intervals appeared too wide and contained the true value too often, resulting in empirical levels above 95%. This situation results because the estimators for the standard error were biased high (Fig. 9); thus, this overestimated estimator counteracts the zero and mean–variance correlation problems discussed earlier. The interaction seemed to work in our favor for the intermediate run sizes, but the overestimated variance dominated for larger run sizes (accuracies >95%), while the zero problem dominated for the smaller run sizes (accuracies <95%).

The reasons for the failure of these estimators were not intuitive. Systematic designs perform well because their implicit spatial balance avoids bad samples that occur under many of the other designs — bad samples being those that have all the sampled locations occurring in some small or limited portion of the watershed. These bad samples with poor spatial balance across the entire sampled universe are possible in designs like SRS. Since the naive standard error estimator based on SRS (eq. 3) assumes that every sample is possible, including these bad samples, it tends to overestimate the standard error of the systematic samples and is therefore biased for these designs. The properties of the neighborhood estimator, on the other hand, vary depending on the sampling proportion and the stochastic nature of the population response. These factors interact because the neighborhoods are not defined by the responses of points within some fixed radius in space, but rather the population responses measured at the four closest points. For high sampling fractions, the estimator for the variance will depend on an average of sampled points very close together, which one might expect to be relatively well correlated, all else being equal. However, when sampling a small proportion of the watershed, the neighborhood is made up of observations farther apart and is therefore expected to be less correlated. Additionally, as the response becomes increasingly stochastic, spatial correlation will fall faster for a given increase in neighborhood size, and as a result the standard error estimator will increase even more quickly. Furthermore, Stevens and Olsen (2003) report that if the population has no spatial structure, the local estimates of variance estimate the plan-

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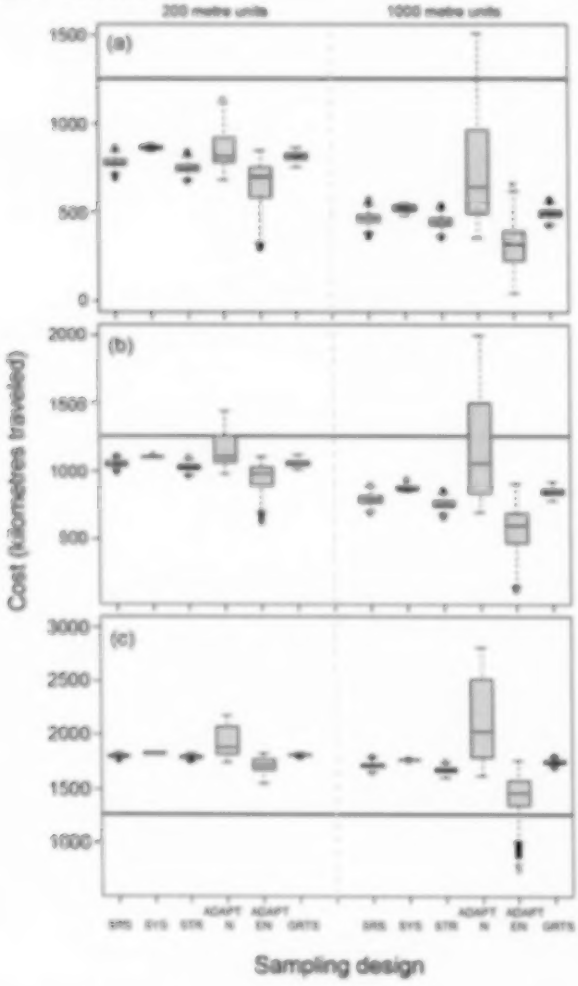
Fig. 7. Distribution of costs (eq. 8) for the sampling strategies: (*a*) 0.05 sampling fraction, (*b*) 0.1 sampling fraction, and (*c*) 0.29 sampling fraction. The solid horizontal line is the cost of index sampling (1254.4 km).



ning variance and hence the average of these is a good estimator; however, it may overestimate the variance if the population is clustered (Stevens and Olsen 2003).

The bias in these estimators suggests that when employing an SYS design, use the successive difference estimator (eq. 4) during small runs and the neighborhood estimator (eq. 5) during large runs. However, even when implementing such a complicated strategy, the benefit is marginal, since there is still a substantial relative bias that consistently exceeds 0.05 (Fig. 9).

STR has other benefits

Stratifying by index performed well in terms of its precision and accuracy and has the added benefit of providing estimates for the number of redds in the index reaches with a precision controlled by the sampler (by allocating the samples intelligently). This advantage is extremely important for many managers, as the resulting estimate can be used to continue the long time series of index samples that may exist (50+ years in the MFSR). For stratified designs, however, allocation of sampling units to different strata will be problematic. Optimal allocation, as used here, is not equal to proportional allocation and is only coincidentally close to equal allocation. Equal allocation is not recommended, but optimal allocation requires information that is typically unknown. In areas where there are few index reaches, an allocation that allows a census of the index stratum seems logical. However, in areas like the MFSR, where the index sites make up almost 30% of the watershed, a census will be difficult if not impossible, and it is not clear how to decide on allocation.

ACS

It is surprising that the ACS strategy did not perform better. ACS is expected to perform well in the case of a rare, clustered population (Thompson 1983), which seems to describe the redd distributions we observed. There are several possible explanations for this failure. The first is that the scale of the sampling unit and the clustering do not correspond. For example, if the scale of the clustering is much larger than the sampling unit, finding a redd in a unit from the original sample does not indicate that the adjacent units are likely to contain redds. A similar problem occurs when the opposite mismatch occurs. The idea of designing an ACS based on characteristics (scale) of the point process has been explored elsewhere (Thompson 1983). A second possible reason that ACS did poorly is that in small-run years, when the clustering is most apparent, the initial sample rarely contains redds and does not meet the criteria for sampling the adjacent units; while in the large-run years the redds are no longer strongly clustered, overestimating the number of redds. ACS also suffers from more practical issues, such as the design makes planning difficult because the final sample size is unknown. This complicates predicting costs, and it makes it difficult for crews to plan trips when they have no idea how long a region will need to be sampled on any one day. Furthermore, the estimator's and sample's complexity may make trend estimation and sharing the data with others difficult.

Segments vs. points

We sampled segments of streams rather than points on the stream network. To sample segments requires frame construction in advance of sampling, which might be prohibitive. However, segmenting the network beforehand leads to the relative simplicity of a finite population and a situation in which many of the ambiguities that can arise during frame construction (such as how to deal with confluences and edge effects) being addressed before sampling begins. In contrast, the EPA recommends an alternative approach, whereby points are sampled from an infinite set along the stream network, and then measurement units (the stream reaches) are defined around each selected point. The point strategy does not require initial frame development, but it adds complications such as the possibility for an infinite number of sampling units, overlapping measurement units, ambiguity at confluences, and measurement units extending beyond the edge of the universe or strata (Stevens and Urqu-

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Table 4. Precision for strategies keeping costs fixed so that 95% of the samples have cost less than or equal to 1253.4 m (i.e., the cost of the index strategy).

		Run size								
Strategy	*n*	20	83	110	318	424	661	1730	1789	2271
200 m units										
SRS	476	63.1	30.0	28.9	19.3	16.1	13.3	11.4	11.8	10.4
SYS*	458	59.4	29.6	30.4	14.8	13.8	11.3	7.8	7.5	6.9
GRTS *	467	60.0	30.5	28.0	15.4	12.1	9.5	9.1	7.7	7.1
STR	486	47.0	25.3	23.3	15.0	14.1	11.6	10.0	10.8	8.8
Adaptive-n	258–478	63.0	29.7	27.8	19.2	16.1	13.6	12.5	13.0	12.4
1000 m units										
SRS	123	64.1	31.7	33.2	25.2	21.4	17.6	16.8	17.8	16.0
SYS*	116	61.1	33.8	31.7	20.7	14.2	10.8	11.8	13.8	10.5
GRTS *	122	48.5	23.3	31.1	18.4	21.5	13.1	14.4	12.2	10.8
STR	130	41.9	22.8	22.4	16.2	16.4	13.8	12.9	14.3	11.9
Adaptive-n	31–122	63.7	89.8	29.6	25.3	24.2	22.3	23.3	25.2	25.1

Note: Precision is measured by the coefficient of variation × 100 (eq. 7). The most precise strategies for each column (run size) are shaded; when more than one strategy is highlighted within a column, the difference in precision is unclear because of simulation error. SRS, simple random sampling; SYS, systematic sampling; GRTS, spatially balanced design; STR, stratified sampling; Adaptive-n, adaptive cluster sampling when *n* = the original sample size.

*Precision is evaluated through simulation.

hart 2000). Some of these complications can lead to inadvertent unequal probability designs, although many of these issues have been resolved (see for example Stevens and Urquhart 2000). If a particular watershed will be sampled every year, then spending the effort to create a finite sampling frame in advance might be worth it, but if the sampling is to occur only once, the additional work is unlikely to be cost effective.

The cost function

In constructing a cost function, we made a number of simplifications to the reality of conducting redd surveys in remote locations. The cost function we used is necessarily simple and particular to one implementation in the MFSR. Indeed, given that the MFSR is censused with helicopter surveys, our choices were de facto arbitrary. There are myriad cost functions that account for diverse modes of transport and eccentricities of specific watersheds; however, we needed a cost function that was relatively realistic in accounting for the choices researchers were likely to make in other watersheds — primarily balancing numbers of access points and travel by foot with total number of samples. The cost function we used did not include or assume equal travel to all access sites; because some sections of the MFSR are remote, these costs might be substantial or differ substantially. The cost function did not account for crew trips. When there are many sample sites at a particular access point, crews might need to camp or visit the site more than once. Crews cannot remain on site indefinitely and additional costs accrue if the crews have to camp overnight. Additionally, this cost function is specific to a watershed where roads are not common. In watersheds where roads are common, crews might hike from the road to individual sites and back again, essentially driving from site to site. Road distance and the distance from the road to the sites rather than distance along the network would be important in that case. However, in spite of the various specifics of the cost function we used, analyzing sampling effort was useful in demonstrating the approach to balancing statistical precision with allocated resources in the design process.

Sampling larger areas

It is possible that these designs will not perform competitively when scaled up to larger areas. Although there is no evidence that these designs are scale-dependant, most large-scale designs will be more complex, having two or several stages of sampling. Currently there are several large-scale, multistage monitoring programs implemented in the Pacific Northwest to assess the health of endangered anadromous fish populations and (or) their habitat. These programs involve numerous federal, state, and local management authorities that have diverse mandates to monitor stream networks. An important feature of these sampling designs is that in each case, sampling is a two-step process. In the first step, large sampling units (e.g., level 6 HUCs) are chosen with some form of randomization scheme. In the second step, stream reaches within the selected HUCs are selected. This second stage is where our results can be applied.

Recommendations

Sampling objectives and resources (budget) should first dictate which strategy is appropriate. For example, if precise estimates of status within the index region are necessary, then the STR strategy should be used. After these considerations, this study suggests sampling as many small units as possible and that designs that implicitly spread the sample out in space are most precise (SYS or GRTS), but there is an advantage to stratifying by the index reaches during small runs. Stratifying by index reaches demonstrated consistently competitive performance under the range of observed conditions, even if performance was not outstanding under any circumstance; this suggests that some form of stratification is a reasonable basic design template. This generally good alternative will also benefit from reduced costs (although modestly) when oversampling the easy-to-access index stratum. However, while some form of stratification

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Table 5. Precision per average cost in 1/(km traveled) × 1000 (eq. 9).

	Run size								
Strategy	20	83	110	318	424	661	1730	1789	2271
(*a*) Sampling fraction = 0.05.									
200 m units (n = 170)									
SRS	1.16	2.43	2.52	3.79	4.54	5.49	6.41	6.19	7.00
SYS*	1.07	2.23	2.29	4.31	5.06	5.64	7.84	7.70	8.58
GRTS *	1.28	2.45	2.48	3.60	4.87	5.27	7.36	6.93	8.93
STS	1.54	2.90	3.14	4.87	5.26	6.38	7.46	6.88	8.42
Adaptive-n	1.16	2.46	2.62	3.85	4.67	5.57	6.28	6.04	6.28
Adaptive-En	1.15	2.45	2.61	3.80	4.60	5.51	6.42	6.26	6.55
1000 m units (n = 35)									
SRS	1.67	3.37	3.22	4.24	6.01	6.08	6.37	6.01	6.70
SYS*	1.66	3.22	3.06	4.48	4.89	6.48	6.92	6.03	7.69
GRTS *	3.10	4.28	2.81	9.52	5.68	8.26	8.43	8.04	11.15
STR	2.38	4.50	4.55	6.22	6.37	7.66	8.19	7.41	8.84
Adaptive-n	1.67	3.56	3.40	4.03	4.04	4.33	4.13	3.81	3.73
Adaptive-En	1.71	3.86	3.76	5.05	5.37	6.50	7.34	6.68	7.11
(*b*) Sampling fraction = 0.1.									
200 m units (n = 340)									
SRS	1.24	2.61	2.72	4.06	4.87	5.89	6.88	6.64	7.51
SYS*	1.31	2.32	3.23	5.42	5.62	6.33	8.67	8.84	9.96
GRTS *	1.44	2.68	2.72	4.29	6.20	7.11	8.27	8.54	9.46
STR	1.66	3.10	3.36	5.23	5.61	6.80	7.94	7.31	8.98
Adaptive-n	1.24	2.65	2.82	4.13	4.98	5.95	6.70	6.47	6.93
Adaptive-En	1.24	2.63	2.86	4.04	4.84	5.71	6.25	6.02	6.08
1000 m units (n = 69)									
SRS	1.40	2.84	2.72	3.57	4.22	5.12	5.36	5.06	5.61
SYS*	1.40	2.92	2.99	4.81	5.12	5.79	6.73	5.94	6.67
GRTS *	3.04	3.94	2.47	5.47	4.95	6.40	6.92	7.66	6.65
STR	2.04	3.86	3.88	5.35	5.44	6.54	6.99	6.32	7.55
Adaptive-n	1.41	3.00	2.87	3.48	3.59	3.94	3.88	3.70	3.62
Adaptive-En	1.43	3.15	3.05	3.96	4.22	1.93	5.38	4.91	5.20
(*c*) Sampling fraction = 0.29.									
200 m units (n = 1000)									
SRS	1.41	2.96	3.07	4.60	5.52	6.67	7.79	7.52	8.51
SYS*	2.34	3.35	4.68	5.72	5.94	7.22	9.50	12.24	13.65
GRTS *	1.49	2.88	3.11	5.31	6.89	8.88	9.31	9.80	12.64
STR	2.05	3.62	3.98	6.24	6.42	7.76	9.00	8.20	10.29
Adaptive-n	1.41	2.99	3.19	4.68	5.66	6.80	7.95	7.70	8.48
Adaptive-En	1.41	2.98	3.17	4.61	5.53	6.56	7.37	7.02	7.50
1000 m units (n = 204)									
SRS	1.26	2.56	2.44	3.21	3.80	4.61	4.83	4.56	5.06
SYS*	1.13	2.66	3.48	4.67	5.55	7.42	7.81	8.42	8.33
GRTS *	1.42	2.90	2.71	4.28	4.35	5.41	5.19	6.77	6.64
STR	2.10	3.70	3.85	5.35	5.04	5.94	6.35	5.71	6.95
Adaptive-n	1.27	2.71	2.61	3.30	3.62	4.26	4.47	4.49	4.48
Adaptive-En	1.27	2.72	2.61	3.27	2.49	3.91	3.90	3.70	3.66

Note: Larger numbers indicate the most cost-effective strategies. SRS, simple random sampling; SYS, systematic sampling; GRTS, spatially balanced design; STR, stratified sampling; Adaptive-n, adaptive cluster sampling when n = the original sample size; Adaptive-En, adaptive cluster sampling when n = the expected final sample size.

*Precision evaluated through simulation.

is recommended, there are still a number of design decisions within and between strata. What one does within strata is another matter. Given that the SYS and GRTS strategies performed consistently better than SRS, either of these designs should be used within each stratum. As for allocation of sampling resources to the two strata, oversampling the index reaches is appropriate for three reasons: (*i*) the estimators for the status within the index region will be more precise so that the long time series can be continued; (*ii*) the status estimators for the entire watershed will be more

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Fig. 8. Problems with accuracy for all designs. (*a*). The sampling distribution of the estimate of status for simple random sampling (SRS) of 170 200 m units during 1995. 43.7% of the samples contained no redds, resulting in estimates of status and standard error equal to zero. When this happened, the confidence interval was also zero. The true value, 20 redds, is marked by the vertical line. (*b*) Estimates of the total number of redds and its standard error from SRS 170 200 m units during 2002. These display a positive correlation of 0.83. Solid points indicate iterations whose confidence interval contained the true value, while open point iterations did not; only 93.2% of the points are solid, indicating that this strategy is not accurate despite theoretical considerations. The open triangle locates the true values: 1789 redds and standard error 342.1.

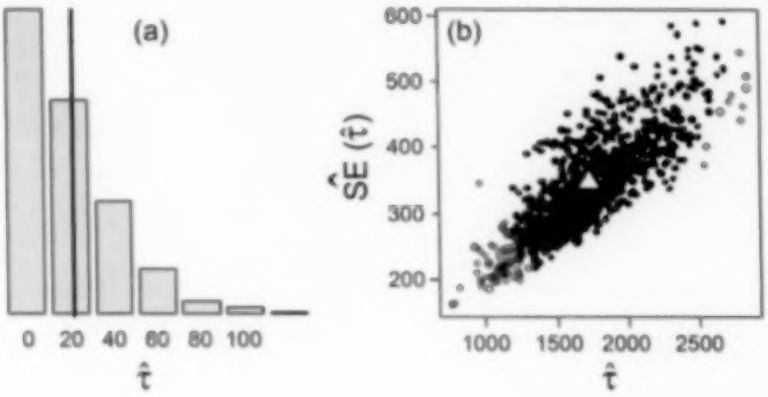
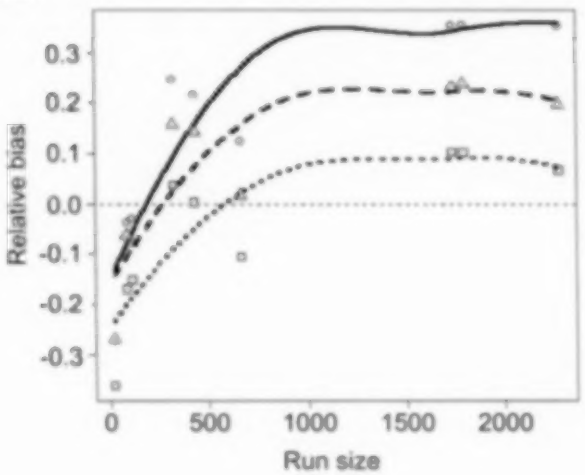


Fig. 9. Relative bias for the standard error for systematic sampling with $n = 170$ (sampling proportion 0.05 and 200 m units). The lines are smooth lines (LOESS, Cleveland 1979) to show the trends. The bias of the estimators depends on the run size, with all three showing negative bias during small runs and positive bias during large runs.



precise; and (*iii*) costs will be lower. Finally, it should be noted that while the focus of this work was on the design of sampling schemes for aquatic resources on river networks, Chinook salmon redds in particular, it would not have been possible to do these analysis were it not for the time series of censuses in the MFSR. As such, for large-scale monitoring program design, we recommend one census-based data collection if possible to serve in sampling design guidance and assessment.

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Predation by brown trout (*Salmo trutta*) along a diversifying prey community gradient

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Abstract: Predation has a fundamental role in aquatic ecosystems, but the relative importance of factors governing prey selection by predators remains controversial. In this study, we contrast five lakes of a subarctic watershed to explore how prey community characteristics affect prey selection and growth rate of the common top predator, brown trout (*Salmo trutta*). The lakes constitute a distinct gradient of different coregonid prey fish, ranging from monomorphic common whitefish (*Coregonus lavaretus*) to polymorphic whitefish co-occurring with vendace (*Coregonus albula*). The brown trout was a morph–species- and size-specific pelagic predator, selecting the small-sized, pelagic whitefish morph or vendace over the benthic whitefish morphs. In all lakes, the average prey size increased with predator size, but small-sized prey were also included in the diet of large predators. The selection of small-sized, pelagic prey fish appeared to be a favourable foraging strategy for the brown trout, yielding higher growth rates and an earlier ontogenetic shift to piscivory. The findings emphasize that piscivory appear to be shaped by the diversity, size-structure, and abundance of available prey in a given community.

Résumé : La prédation joue un rôle fondamental dans les écosystèmes aquatiques, mais l'importance relative des facteurs qui déterminent la sélection des proies par les prédateurs reste un sujet controversé. Dans notre étude, nous comparons cinq lacs d'un bassin versant subarctique afin de déterminer comment les caractéristiques de la communauté de proies affectent la sélection des proies et le taux de croissance du prédateur supérieur commun, la truite brune (*Salmo trutta*). Les lacs forment un gradient marqué de proies constituées de divers poissons corégonidés, allant de corégones lavarets (*Coregonus lavaretus*) monomorphes à des corégones lavarets polymorphes cohabitant avec des corégones blancs (*Coregonus albula*). La truite brune est un prédateur pélagique qui choisit ses proies en fonction de la forme–espèce et de la taille et qui préfère la forme pélagique de petite taille du lazaret et le corégone blanc au lazaret benthique. Dans tous les lacs, la taille moyenne des proies augmente en fonction de la taille des prédateurs, mais les proies de petite taille font aussi partie du régime des grands prédateurs. La sélection de poissons pélagiques de petite taille comme proies semble être une stratégie bénéfique chez la truite brune, car elle permet des taux de croissance plus élevés et un passage ontogénique à l'ichtyophagie plus précoce. Ces résultats soulignent le fait que l'ichtyophagie semble être déterminée par la diversité, la structure en taille et l'abondance des proies disponibles dans une communauté donnée.

[Traduit par la Rédaction]

Introduction

Predator–prey interactions are essential for the population dynamics of both predator and prey (e.g., Sinclair et al. 2003; Myers et al. 2007; Persson et al. 2007). Most predators are selective feeders, having a diet that constitutes only a subset of the available prey (reviewed by Stephens and Krebs 1986). The feeding selectivity of the predator is influenced by the relative species composition of the prey community, and predators are anticipated to select prey that provide an optimum energy gain relative to the time spent on foraging (Stephens and Krebs 1986; Sih and Christensen 2001). Diet selection depends on characteristics of both the predator (e.g., morphological adaptations) and the prey (e.g., energetic value, predation susceptibility), and predators may furthermore exhibit functional responses where their consumption rate is influenced by the prey abundance (Abrams and Ginzburg 2000). Hence, several factors may

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contribute to the feeding patterns of a predator, and potential outcomes may range from predators feeding randomly to predators that feed highly selectively on specific prey (Eggers 1977; Sih and Moore 1990). Although these basic mechanisms of predator–prey interactions are of major interest in aquatic ecology (reviewed in Werner and Gilliam 1984; Sih and Christensen 2001), they are often difficult to study comprehensively in natural communities (Roughgarden 1986; Kramer et al. 1997).

In lakes, predation by piscivorous fish may affect the prey fish communities directly (i.e., by reducing prey fish density or altering size structure; Persson et al. 1996) or indirectly by determining prey fish behaviour with respect to foraging, habitat use, shoaling, diurnal activity patterns, or growth (Turner and Mittelbach 1990; Lima 1998). Habitat utilization is an important factor in predator–prey interactions (Persson and Greenberg 1990; Byström et al. 2003) and, in contrast to the open-water pelagic habitat, the littoral and profundal zones of lakes may provide refuges for prey fish in terms of structural complexity and darkness, respectively. Predator–prey relationships are also highly size dependent (Juanes 1994; Persson et al. 1996; Scharf et al. 2000). Because of gape-size limitations, predatory fish usually experience an ontogenetic diet shift from invertebrates to fish at a certain size depending on availability, size, and species-specific characteristics of the prey (Werner and Gilliam 1984; Mittelbach and Persson 1998). Some prey fish may, on the other hand, be able to grow out of the "predation window" (i.e., the size range where they are vulnerable to predation; Claessen et al. 2002). Different prey species may furthermore have different growth trajectories, leading to different time frames of predation susceptibility. However, studies combining field data on prey diversity, size structure, and abundance with prey utilization of top predators are scarce.

Subarctic lakes in northern Europe usually represent relatively pristine, low-diversity ecosystems often dominated by salmonid fish. Brown trout (*Salmo trutta*) is a common top-predator in many of these lakes, particularly in systems dominated by two closely related coregonid fish (common whitefish (*Coregonus lavaretus*) and (or) vendace (*Coregonus albula*)), where the brown trout may reach a large body size through piscivory (Næsje et al. 1998; Vehanen et al. 1998). The coregonids in these northern lakes exhibit extensive polymorphism and highly variable life histories (Kahilainen et al. 2003; Kahilainen et al. 2005; Amundsen et al. 2004*a*) and likely constitute heterogeneous prey assemblages for the piscivorous brown trout, potentially resulting in contrasting predator–prey interactions.

This study compares the predator–prey relationships of brown trout and coregonids between five lakes of the subarctic Paatsjoki–Pasvik watershed in northern Europe. Three whitefish morphs have been identified in this watershed (Amundsen et al. 2004*b*; Kahilainen and Østbye 2006, Østbye et al. 2006), and vendace is also present as an introduced, non-native species in the lower reaches (Amundsen et al. 1999). The five lakes therefore comprise a gradient of different coregonid prey communities for the brown trout, including one lake with a single whitefish morph present, two lakes inhabited by three sympatric morphs, and two lakes where the whitefish morphs co-occur with vendace. These study lakes in the same watershed thus enable comparisons of predator–prey interactions along a gradient of increasing diversity of coregonid prey in otherwise similar lakes. The following hypotheses were tested: (*i*) the predator (i.e., brown trout) preys selectively on coregonids and prefers the habitat with the most profitable prey community; (*ii*) the predator switches to piscivory at smaller sizes if the prey community includes abundant, small-sized prey; (*iii*) prey size selection is a positive function of predator size; and (*iv*) predator growth rate is positively correlated with the density of potential prey in the environment.

Materials and methods

Study sites and fish communities

The headwaters of the Paatsjoki–Pasvik watershed (68°–69°N, 26°–30°E) discharge into Lake Inari (surface area 1102 km^2) in northern Finland, run throughout Russia for 30 km, and finally form the border between Norway and Russia for a distance of approximately 120 km before entering the Arctic Ocean (Fig. 1). The total catchment area of the watershed is 18 403 km^2. The five lakes in the present study are Lake Vuontisjärvi (referred to as Lake 1), Lake Muddusjärvi (Lake 2), and Lake Paadar (Lake 3) on the Finnish side and Lake Skrukkebukta (Lake 4) and Lake Vaggatem (Lake 5) on the Norwegian side. The surface area of the lakes varies from 7 to 48 km^2, with maximum and mean depths of 30–73 m and 6.5–14 m, respectively (Table 1). All the lakes are oligotrophic (total phosphorus (totP) = 6–9 μg·L^{-1}, total nitrogen (totN) = 145–170 μg·L^{-1}), neutral (pH of 6.8–7.2), and with some humic impacts (Secchi depths between 3 and 8 m). The ice-free season in the lakes lasts from May–June to October–November.

All study lakes have a coregonid-dominated fish fauna. Beside coregonids and brown trout, the most common fish species include European perch (hereafter referred to as perch; *Perca fluviatilis*), northern pike (*Esox lucius*), burbot (*Lota lota*), grayling (*Thymallus thymallus*), ninespine stickleback (*Pungitius pungitius*), and Eurasian minnow (*Phoxinus phoxinus*) (Table 1). Brown trout is the most abundant salmonid predator in all lakes, consisting of both stocked (>60% of the catches in all lakes) and native fish (Kahilainen and Lehtonen 2002; Jensen et al. 2004). Stocked and native fish are approximately equal in size (±20 cm) at the start of the first growing season in the lake during early summer (Kahilainen & Lehtonen 2001). In the present study, the native and stocked brown trout have been pooled in the analyses, as they have similar diet preferences and growth patterns (Kahilainen and Lehtonen 2001; Jensen et al. 2004).

The whitefish occur as three morphologically and ecologically distinct morphs. Adaptive radiation and incipient ecological speciation is a likely explanation for the adaptive evolution of these whitefish morphs (Østbye et al. 2006), and in this study the morphs are considered as different biological species. In allopatry, the large sparsely rakered (LSR) whitefish has a wide niche utilizing all principal habitat types and prey (Amundsen et al. 2004*a*; Kahilainen et al. 2007). In sympatry, each whitefish morph is specialized to one principal niche, including a profundal-dwelling benthivore (i.e., the small sparsely rakered whitefish (SSR

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Fig. 1. (*a*) Map of Northern Europe showing the location of the Paatsjoki–Pasvik watershed. (*b*) Map of the Paatsjoki–Pasvik watershed indicating the location of study Lakes 1–5.

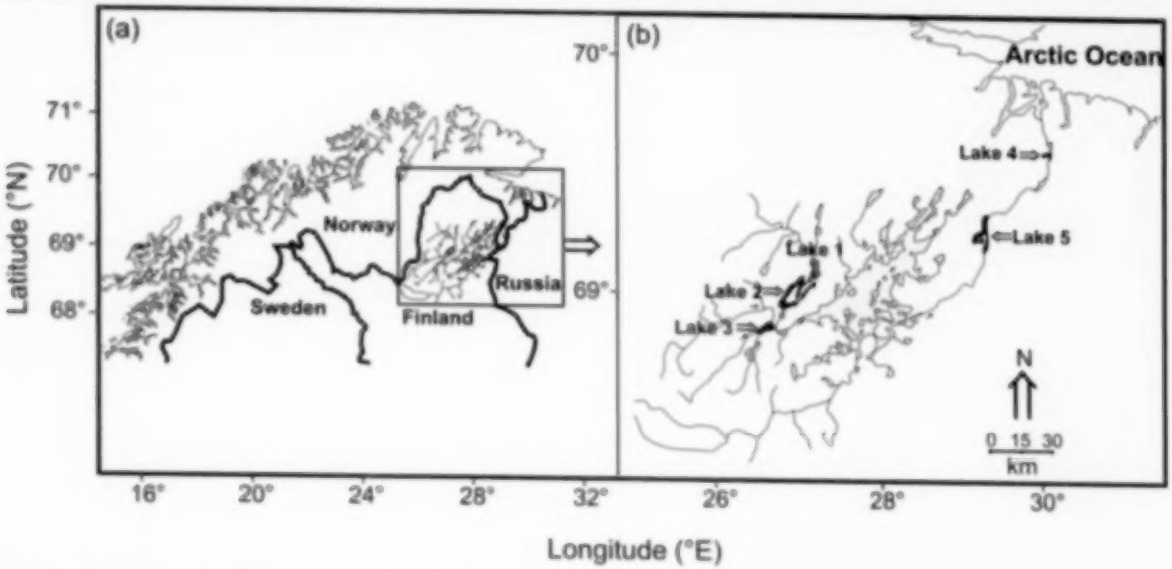

Table 1. Abiotic and biotic background data from the five study lakes.

Parameter	Lake 1	Lake 2	Lake 3	Lake 4	Lake 5
Latitude (°N)	69°01′	69°00′	68°52′	69°33′	69°14′
Longitude (°E)	27°04′	26°50′	26°35′	30°07′	29°15′
Country	Finland	Finland	Finland	Norway	Norway
Surface area (km^2)	11	48	21	7	15
Altitude (m above sea level)	151	146	144	21	52
Maximum depth (m)	31	73	56	38	30
Mean depth (m)	6.5	8.5*	11.7	14	4
Secchi depth (m)	8	3	6*	4–5.5	3–4.5
Color (mg Pt·L^{-1})	8*	15*	15*	16	17
pH	7.2*	7.2*	7.1*	6.9	6.8
Total P (μg·L^{-1})	7*	5*	6*	7	9
Total N (μg·L^{-1})	170*	160*	160*	156	145
Coregonid species and morphs	LSR	LSR, SSR, DR	LSR, SSR, DR	LSR, DR, VEN	LSR, DR, VEN
Other fish species	b, c, d, e, f, g, h	a, b, c, d, e, f, g, h	b, c, d, e, f, g, h	b, c, e, f, g, h	b, c, e, f, g, h

Note: Other fish species present in the study lakes in addition to brown trout are indicated with abbreviations: LSR, large sparsely rakered whitefish (*Coregonus lavaretus*); SSR, small sparsely rakered whitefish, DR, densely rakered whitefish; VEN, vendace (*Coregonus albula*); a, Arctic char (*Salvelinus alpinus*); b, grayling (*Thymallus thymallus*); c, Eurasian minnow (*Phoxinus phoxinus*); d, threespine stickleback (*Gasterosteus aculeatus*); e, ninespine stickleback (*Pungitius pungitius*); f, European perch (*Perca fluviatilis*); g, northern pike (*Esox lucius*); h, burbot (*Lota lota*).

*Data from Lapland Regional Environment Centre, P.O. Box 8060, FIN-96101 Rovaniemi, Finland.

whitefish)), a littoral-dwelling benthivore (i.e., LSR whitefish), and a pelagic planktivore (i.e., the densely rakered whitefish morph (DR whitefish)) (Amundsen et al. 1999, 2004*a*; Kahilainen et al. 2004). Lake 1 is inhabited by a single LSR morph, whereas all three whitefish morphs (SSR, LSR, and DR) occur in sympatry in Lakes 2 and 3 (Kahilainen et al. 2004). In Lakes 4 and 5, the sympatric whitefish morphs co-occur with an introduced non-native coregonid species, the vendace, which has become a highly abundant pelagic species after invading these lakes in the early 1990s (Amundsen et al. 1999; Bøhn and Amundsen 2001, Bøhn et al. 2004). The somatic growth rates differ between the whitefish morphs, being highest in LSR whitefish, intermediate to low in the DR whitefish, and lowest in the SSR whitefish (Kahilainen and Lehtonen 2003; Bøhn and Amundsen 2004). The vendace in Lakes 4 and 5 have very slow growth rates, attaining maximum sizes well below 15 cm (Bøhn et al. 2004).

Field sampling

A total of 2430 brown trout were sampled throughout June to October in 1998–2004 by gill nets and fishing rods (sampling details in Kahilainen and Lehtonen 2003; Jensen et al. 2004, 2006). The total lengths and weights of the fish were measured to an accuracy of 1 mm and 1 g, respectively, and stomachs were removed and frozen (–20 °C) for further analysis. In addition, scales and otoliths were taken for age determination.

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Prey fish samples were collected from the study lakes during September in 1998–2004. For prey fish sampling in Lakes 1–3, gillnet series with mesh sizes (knot to knot) of 12, 15, 20, 25, 30, 35, 45, and 60 mm were used in the littoral and profundal habitats, and a small pair trawl (5 m high, 8 m wide, and cod-end mesh size 3 mm) was used in the pelagic habitat (details in Kahilainen et al. 2004). In Lakes 4–5, prey fish were caught in the littoral and profundal habitats using bottom gillnet series with mesh sizes of 10, 12.5, 15, 18.5, 22, 26, 35, and 45 mm; in the pelagic habitat, floating gillnet series with mesh sizes of 8, 10, 12.5, 15, 18.5, 22, 26, and 35 mm were used.

Prey fish were identified to species and whitefish to morph according to head and gillraker morphology (Amundsen et al. 2004*a*; Kahilainen and Østbye 2006). The total lengths and weights of the prey fish were determined to an accuracy of 1 mm and 1 g, respectively. Habitat use of coregonids was evaluated using catch per unit effort (CPUE based on number of caught fish) of different morphs–species in the littoral, profundal, and pelagic habitats (details in Kahilainen et al. 2004; Amundsen et al. 2004*a*). Coregonids were the dominant fish species in all the study lakes (proportion in catches > 80% in every lake), and the subsequent analyses were concentrated only on this prey resource.

To assess the density of pelagic coregonids, areas deeper than 6 m were sampled using a SIMRAD EY-500 echosounder equipped with downfacing split-beam transducers operating at 120 kHz frequency (ES120-7F in Lakes 1–3 and ES120-4 × 10 in Lakes 4 and 5). Transects were placed equidistantly in Lakes 1–3 (Kahilainen et al. 2004), whereas a combination of zigzag and parallel transects was applied in Lakes 4 and 5. Details of equipment and settings are described in Kahilainen et al. (2004).

Laboratory and data analyses

The prey items in brown trout stomachs were identified as far as possible. Prey fishes were identified to species by the remaining external features, and whitefish were identified to morph by gillraker examination (Kahilainen and Lehtonen 2002; Amundsen et al. 2004*b*). Fish prey other than coregonids (e.g., ninespine sticklebacks, perch, Arctic char, and burbot) were pooled as other fish, whereas aquatic insects (including Ephemeroptera, Trichoptera, Plecoptera, Odonata, Chironomidae, and Coleoptera) were pooled as invertebrates. Prey abundance (A_i, percent volume), or the percentage of each diet category in the stomachs (sum of all categories = 100%), was calculated as follows:

$$A_i = \sum S_i / \sum S_{ts} \times 100$$

where S_i is fullness for diet category i, and S_{ts} is the total stomach fullness (Amundsen et al. 1996).

The similarity in coregonid composition between the brown trout stomach contents and the proportional coregonid CPUEs from different habitats (littoral, profundal, pelagic) was calculated using Schoener's (1970) index:

$$\alpha = 1 - 0.5\left(\sum_{i=1}^{n} |P_{xi} - P_{yi}|\right)$$

where P_{xi} is the proportion of coregonid species–morph i consumed by brown trout population x, P_{yi} is the proportion of coregonid species–morph i dwelling in habitat y, and n is the number of coregonid taxa in the lake. The index was also used to compare the similarity in brown trout diets between the lakes. The index gives α values from 0 to 1, where 0.00 and 1.00 indicates no overlap and complete overlap, respectively. An index value ≥ 0.60 is considered to represent a biologically significant similarity (Wallace 1981).

The total length of undigested prey fish in the brown trout stomachs were measured to an accuracy of 1 mm, and the length of partially or entirely digested coregonid prey were estimated from the otolith length (Kahilainen and Lehtonen 2001). The average coregonid prey length (log-transformed) in brown trout stomachs was compared statistically between the lakes using analysis of covariance (ANCOVA) with predator length as covariate. Pairwise comparisons were made with Tukey's honestly significant difference (HSD) test. The relationship between coregonid prey and brown trout length was furthermore estimated using linear regression analysis for each lake separately. To develop a general model of the predator–prey length relationship between brown trout and coregonids in the studied lakes, data were pooled from all lakes and we performed a quantile regression analysis, estimating the median and upper (99th quantile) and lower (1st quantile) bounds of the relationship (Cade et al. 1999).

Brown trout age was determined from both scales and otoliths in Lakes 1–3 and from otoliths in Lakes 4–5. The somatic growth rate of brown trout was measured by the annual specific growth rate (G, year^{-1}):

$$G = 100(\ln W_2 - \ln W_1)(t_2 - t_1)$$

where W_2 and W_1 are average body weights in age classes t_2 and t_1, respectively. G was estimated between different age classes for wild fish and between years after stocking for stocked fish. G values of the same age class in different lakes were compared with analysis of variance (ANOVA), and pairwise comparisons between age classes were made with Tukey's HSD test.

Hydroacoustic data were analyzed using EP500 (Lakes 1–3) and Sonar5 (Lakes 4 and 5) postprocessing software. The analysis was started at a depth of 3 m and stopped 0.5 m above the bottom. Integration threshold was –60 dB for all lakes, and all targets were assumed to be coregonids, with the exception of very small fish targets, which were likely ninespine or threespine sticklebacks. These were excluded from the coregonid density estimates by setting the target strength (TS) thresholds between –54 and –59 dB based on TS distributions. The coregonid density of each transect was computed using observed TS distributions (for details see Kahilainen et al. 2004). The mean density in each lake and the variance of the means were computed by taking variable transects length into account (Shotton and Bazigos 1984), and 95% confidence limits were estimated assuming a Poisson distribution (Jolly and Hampton 1990).

Results

Predator diet selection

The brown trout were mainly piscivorous in all lakes. In

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Fig. 2. Diet composition of different total length groups of brown trout (*Salmo trutta*) from the studied Lakes 1–5. The number of examined stomachs containing prey items is indicated above the bars. LSR, large sparsely rakered whitefish (*Coregonus lavaretus*); DR, densely rakered whitefish.

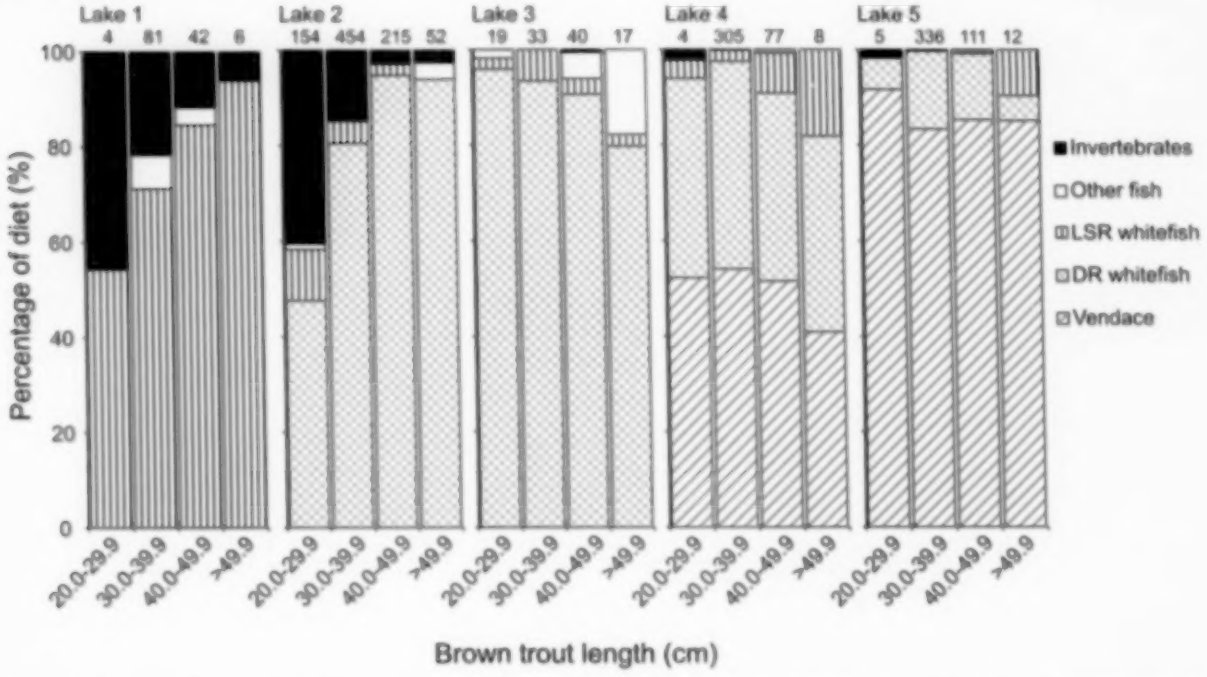

Table 2. Similarity (Schoener's α) between pooled brown trout stomach contents and proportional coregonid catch per unit effort (CPUE) in different habitats of the study lakes.

Habitat	Lake 1	Lake 2	Lake 3	Lake 4	Lake 5
Littoral	1	**0.60**	0.53	0.30	0.20
Profundal	1	**0.76**	**0.75**	**0.62**	0.51
Pelagic	1	**0.95**	**0.96**	**0.80**	**0.93**

Note: Values ≥ 0.60 (shown in bold) are considered to represent biologically significant similarities (except Lake 1 with only one prey type present).

Lakes 1 and 2, an ontogenetic diet shift from invertebrates to fish was observed with increasing brown trout length, but in Lakes 3–5 all examined length groups were almost exclusively piscivorous (Fig. 2). In all lakes, coregonids were the dominant fish prey for the brown trout, and other fish (ninespine stickleback, perch, burbot, and Arctic char) were only occasionally eaten. In Lake 1, brown trout fed on the only available whitefish morph (LSR), whereas the diet shifted to the pelagic DR whitefish in Lakes 2 and 3 with the three sympatric morphs present. In Lake 4, brown trout preyed on DR whitefish and vendace, whereas the predation shifted almost exclusively to vendace in Lake 5 (Fig. 2). The profundal SSR whitefish was not found in any of the brown trout stomachs.

According to Schoener's index (α), the similarity between the coregonid proportions in the predator diet and the fish catches differed between habitats (except in Lake 1, where LSR whitefish was the only coregonid present). In Lakes 2–5, the highest similarity (α = 0.80–0.96) was consistently found for the pelagic habitat (Table 2). The similarity was somewhat lower for the profundal habitat in Lakes 2–4 (α = 0.51–0.76) and was generally the lowest for the littoral habitat of the lakes (α = 0.20–0.60). The brown trout diet similarity between lakes was biologically significant in two cases: between Lakes 2 and 3 (α = 0.99) and between Lakes 4 and 5 (α = 0.69) (Table 2, Fig. 3). In the other comparisons, the brown trout diets were less similar (α < 0.60).

Predator diet versus prey diversity, size distribution, and abundance

The average coregonid prey length in the brown trout stomachs was significantly different between the lakes and showed a decreasing trend from Lake 1 towards Lake 5 (Fig. 3*a*), irrespective of the predator length (ANCOVA, $F_{[4,1793]}$ = 129.4, P < 0.0001). The prey length further differed significantly in all pairwise comparisons between the lakes (Tukey's HSD tests, P < 0.001), except between Lakes 1 and 2 (P > 0.05). In Lake 1, the brown trout stomachs included prey fish larger than those observed in the pelagic habitat, suggesting that feeding to a large extent occurred in the benthic habitats. Accordingly, the pelagic fish density in Lake 1 was the lowest of all the study lakes. In Lakes 2–5, the brown trout tended to select similarly sized (Lakes 2–3) or slightly smaller (Lakes 4–5) coregonid prey than those observed in the catches (Fig. 3). This difference in prey size is likely due to selectivity differences between gill net and pelagic trawl.

There was furthermore a high similarity between the

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Fig. 3. (*a*) Coregonid length distribution in the pelagic catches and in brown trout (*Salmo trutta*) diet in study lakes. Number of samples (*n*) and the average total length (TL) are also indicated. (*b*) Proportion of different coregonids in pelagic catch per unit effort (CPUE; upper circle) and brown trout diet (lower circle) for each lake. (*c*) Coregonid density with 95% confidence limits (upper and lower bound values indicated) in pelagic areas (depth > 6 m) estimated with echosounding.

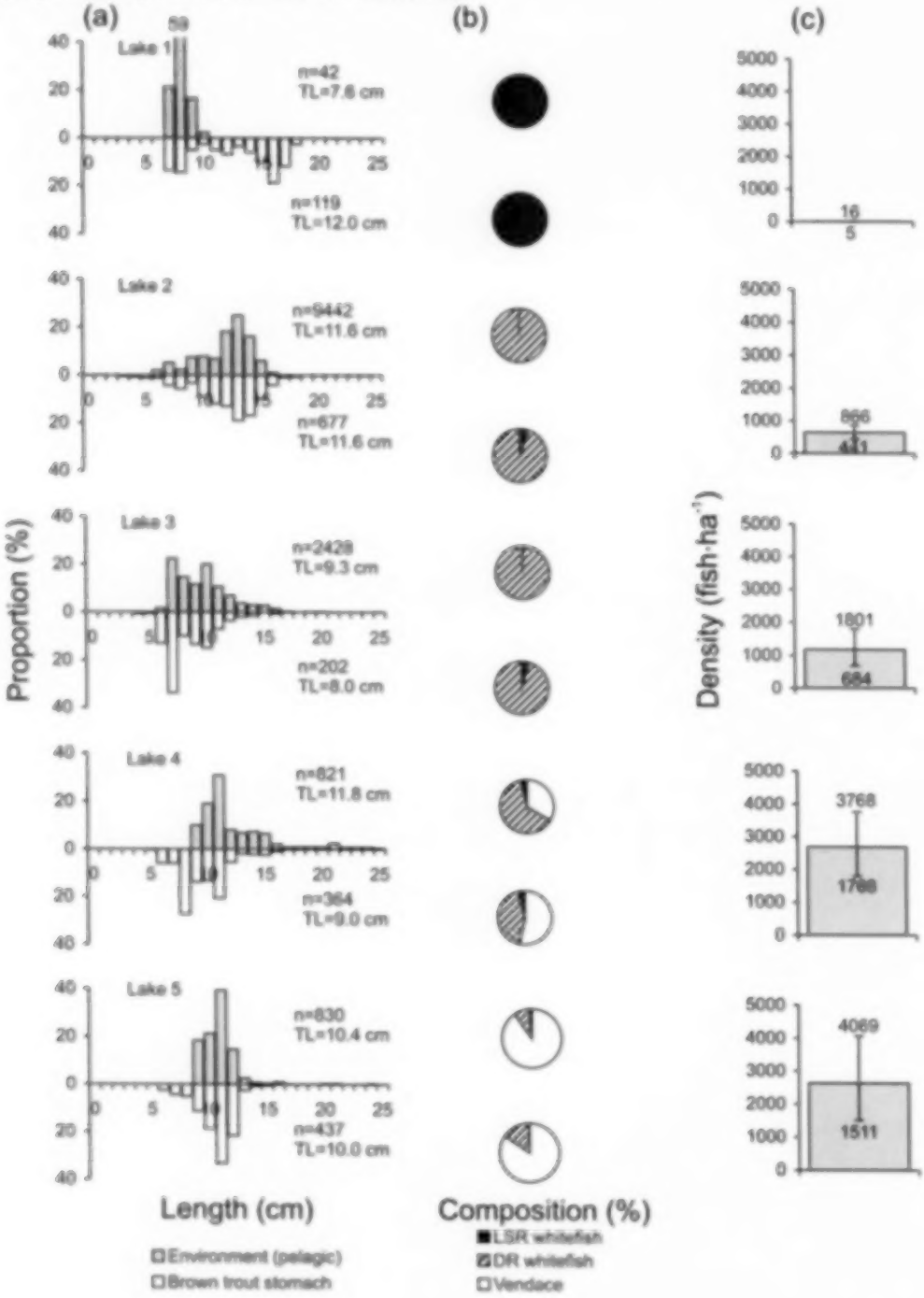

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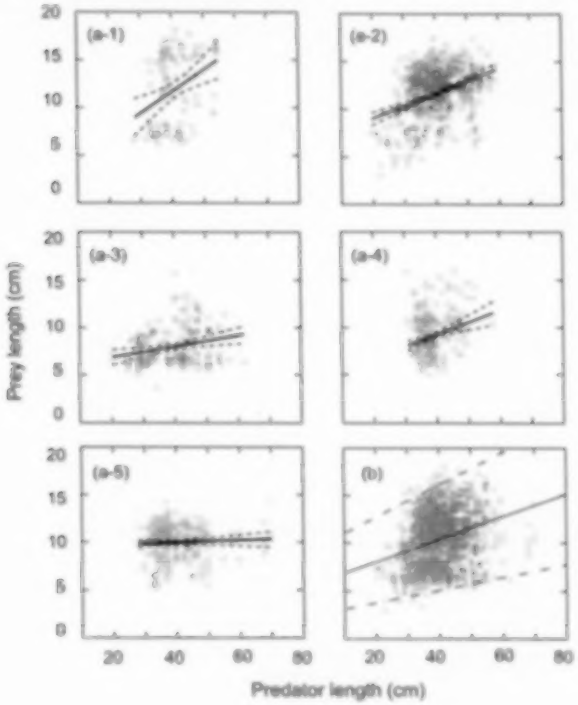
Fig. 4. (*a*-1 to *a*-5) Predator–prey total length relationships in Lakes 1–5 estimated with linear regression analysis. Solid line indicates regression line and broken lines indicate 95% confidence limits. (*b*) Quantile regression of the pooled predator–prey size relationships with median (solid line) and 1% and 99% quantiles (broken lines). The estimated slopes from the quantile regression were 0.12 (median), 0.17 (upper bound, 99% quantile), and 0.07 (lower bound, 1% quantile) ($P < 0.001$).



brown trout diet and the available coregonid prey in the pelagic habitat in all the lakes (Fig. 3*b*, Table 2), and the diets generally reflected the differences in prey communities between lakes. In Lake 1, only LSR whitefish was available; in Lakes 2 and 3, DR whitefish dominated strongly; and in Lakes 4 and 5, DR whitefish co-occurred with vendace. Accordingly, the lakes divided into three distinct groups in terms of the brown trout diet: (1) allopatric LSR was the single prey species in Lake 1, (2) DR whitefish dominated the diet in Lakes 2–3, and (3) vendace and DR whitefish were the most important prey in Lakes 4–5. The mean density of pelagic coregonid prey increased from group 1 (10 individuals·ha^{-1}) to group 2 (640–1180 individuals·ha^{-1}) and peaked in group 3 (2640–2690 individuals·ha^{-1}) (Fig. 3*c*). Differences between the three groups were statistically significant according to the confidence limits of the density estimates.

Predator–prey size relationship

Within all lakes, the length of coregonid fish prey increased significantly with predator size, but the slope of the regression was subject to large between-lake variations (Fig. 4, Table 3). Prey length increased most rapidly with predator length in Lake 1, where the abundance and diversity of coregonid prey was the lowest (Figs. 3 and 4). With the exception of Lake 4, the slopes generally decreased with increasing abundance of small pelagic coregonid prey, and the lowest slope was observed in Lake 5 (Figs. 3 and 4, Table 3).

Table 3. Estimated parameters from linear regressions of the predator–prey total length relationships in the studied lakes.

Lake	*n*	Slope (±95% CL)	Intercept (±95% CL)	r^2	*P*
1	119	0.23±0.11	2.52±4.55	0.12	<0.001
2	677	0.13±0.02	6.38±1.02	0.14	<0.001
3	202	0.06±0.03	5.68±1.28	0.06	<0.001
4	364	0.13±0.05	4.11±1.94	0.07	<0.001
5	437	0.03±0.02	8.66±0.96	0.02	<0.01
1–5	1799	0.11±0.02	5.84±0.72	0.08	<0.001

Note: CL, confidence limit.

In the quantile regressions of the predator–prey length relationship, the median and lower and upper bound slopes all increased significantly with increasing size of the predator (Fig. 4*b*). The range of prey sizes consumed expanded with increasing predator size, as the upper bound exhibited a steeper slope than the lower one. The maximum, median, and minimum prey sizes of a 40 cm predator were estimated to be approximately 16, 10, and 5 cm (i.e., 40%, 25%, and 12%, respectively) of the predator size. For all three parameters, the relative prey length decreased with increasing predator size. The slope of the lower bound (i.e., the 1% quantile) was very low, suggesting a continuum of small-sized coregonid prey in the diet even when the predator attained considerably large sizes.

Predator growth rate

The annual specific growth rate (G) of brown trout during the first lake-year (age class 1) differed significantly between the lakes (ANOVA, $F_{[4,529]} = 9.7$, $P < 0.0001$) and was significantly lower in Lake 1 ($G = 48.9$ g·year^{-1}) compared with the other lakes (range 80.9–93.9 g·year^{-1}; Tukey's HSD tests, $P < 0.0001$) (Fig. 5). Furthermore, there were no significant differences in growth rates between the three age classes of brown trout in Lake 1 (ANOVA, $F_{[2,59]} = 1.3$, $P = 0.274$), whereas there was a significant decrease in G values of age classes 2 and 3 compared with age class 1 in Lakes 2–5 (Tukey's HSD tests, $P < 0.0001$). When comparing the growth rates of age classes 2 and 3, no significant differences were found between the lakes (ANOVA: $F_{[4,216]} = 2.1$, $P = 0.088$ and $F_{[4,112]} = 0.3$, $P = 0.902$, respectively).

Discussion

Individuals of a variety of predator taxa are known to shift habitat and diet to increase foraging gain, and these shifts may be a result of different availability of prey resources and ontogenetic changes in resource use (Werner and Gilliam 1984; Stephens and Krebs 1986). The present study examined different size groups of a predator feeding in five different prey communities. Brown trout larger than 20 cm were highly piscivorous in all the lakes, feeding almost exclusively on coregonid prey fish. A minor exception was

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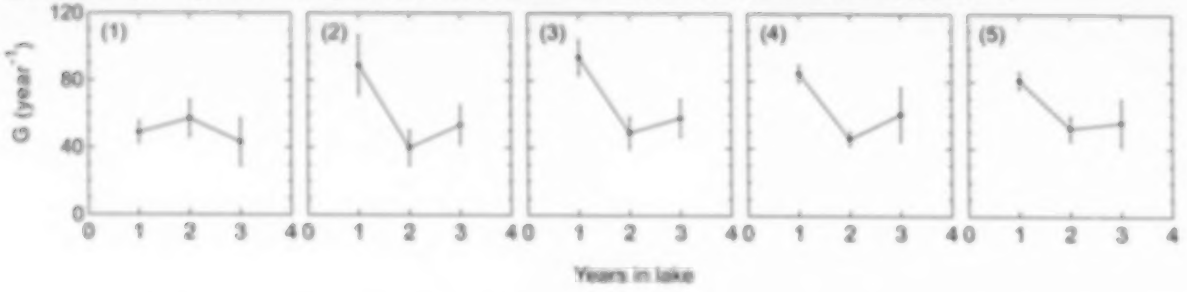
Fig. 5. Annual specific growth rate (G, year^{-1}) of brown trout (*Salmo trutta*) with 95% confidence limits in Lakes 1–5.



represented by the inclusion of invertebrates in the smallest length groups in Lakes 1 and 2. The switch to piscivory in gape-limited predators depends on the availability of small-sized prey fish (e.g., Juanes 1994; Mittelbach and Persson 1998), and the delayed switch to complete piscivory observed in Lakes 1 and 2 was most likely related to a low abundance of small-sized pelagic prey, particularly in Lake 1. In contrast, the brown trout switched earlier to piscivory in Lakes 3–5 with high abundances of pelagic prey available. Our findings are equivalent to the general observations of an ontogenetic niche shift to piscivory at lengths of 20–30 cm in salmonids (Keeley and Grant 2001) and furthermore support the interpretation of pelagic fish as highly preferred prey for piscivorous brown trout.

In general, the foraging patterns were changing from the consumption of a monomorphic and mainly benthic-dwelling coregonid (LSR whitefish in Lake 1) towards the pelagic specialist vendace dominating the diet in Lake 5. This reflects the selective predation by the brown trout. We used Schoener's similarity index to explore the main feeding habitat of the brown trout, and as the highest similarity between the coregonid composition in the environment and in the pooled brown trout diets were found for the pelagic habitat, our data support the conclusion that the brown trout predominantly feeds in the open waters of the lakes. This is also supported by the fact that ninespine sticklebacks and minnows, which are common prey for benthic predators like perch, northern pike, and burbot in the watershed (Amundsen et al. 2003), rarely were observed in the brown trout stomachs. Furthermore, despite the presence of LSR whitefish in all lakes, the piscivorous brown trout in Lakes 2–5 were feeding almost exclusively on DR whitefish and vendace (i.e., the species that predominantly occupied the pelagic habitat of these lakes). In Lake 1 in contrast, the brown trout utilized prey fish larger than those observed in the pelagic habitat, suggesting that the predator chose to forage on larger prey in the benthic habitat when the abundance of small, pelagic whitefish was low. Foraging of piscivorous brown trout has been reported elsewhere to occur in both littoral (e.g., Næsje et al. 1998) and pelagic habitats (e.g., Hyvärinen and Huusko 2006). Our results suggest that the brown trout is a piscivore that may utilize different coregonid prey species in different habitats, but selectively switches to feed on relatively small-sized, pelagic DR whitefish or vendace when these are abundant.

For potential prey species, habitat selection is a trade-off between optimal foraging and predator avoidance behavior (Lima and Dill 1990). In many systems, the most profitable habitat for feeding is also considered to have the highest risk of predation (Werner and Gilliam 1984; Byström et al. 2003). This is obviously the case for DR whitefish and vendace feeding on zooplankton in the pelagic habitat (Bohn and Amundsen 2001; Kahilainen et al. 2007), which is also the prime feeding habitat for the piscivorous brown trout (Kahilainen and Lehtonen 2002). The profundal zone is apparently the least profitable foraging habitat in these lakes and is mainly inhabited by the slow-growing SSR whitefish morph. The low light levels in this habitat provide a good prey refuge from brown trout, and SSR whitefish were never found in the brown trout stomachs. This is in accordance with the general description of brown trout as a visual predator, relying upon good light conditions for efficient predation (Langeland et al. 1991; Schulz and Berg 1992).

A positive relationship between body size of predator and prey has been recognized in a large number of animal taxa (Werner and Gilliam 1984; Wootton 1998; Sinclair et al. 2003). Whereas piscivorous fish are able to ingest prey fish up to approximately 50% of their own length (Juanes 1994), the prey–predator size ratio of 20%–30% found in the present study was close to the average ratios found in other studies of piscivores (Hoyle and Keast 1987; Hambright et al. 1991; Mittelbach and Persson 1998). Our results show a positive relationship between predator size and prey size in all lakes, but the strength of the correlation was dependent on species composition, size structure, and abundance of the prey. The steepest incline in prey size with increasing predator size was seen in Lake 1 (slope = 0.23) where allopatric LSR whitefish was the only coregonid prey fish present, whereas the slope decreased to almost zero in Lake 5, which was dominated by a small-sized, high-abundant vendace population (slope = 0.03). Lake 4 represented an exception in this general trend of predator–prey length slopes, obviously related to a more pronounced availability of larger-sized (>13 cm) pelagic prey than in Lakes 3 and 5.

In Lake 1, the growth rate of brown trout during the first year in the lake appeared to be limited by the low availability of small-sized prey as compared with the other lakes. The growth rates of larger age classes of the predator seemed in contrast not to be limited by the prey size distribution in any of the lakes, as the growth rates of these age classes were similar between all lakes. Thus, although prey size increased with increasing predator size, large predators were not growth-limited by the absence of large prey. First

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year growth and the ontogenetic switch to piscivory were on the other hand clearly enhanced by high abundance of small-sized prey fish. Energetically, a positive correlation between predator and prey size is expected to occur, since larger prey contain more energy than smaller prey, but this may be counteracted by increased energetic costs of searching, pursuing, and handling and also lower capture rates of larger-sized prey (Townsend and Winfield 1985; Crawley and Krebs 1992; Sih and Christensen 2001). When combining all lakes, the quantile regression showed a moderate, positive correlation between brown trout and coregonid prey size. Although this shows that larger predators include larger prey in their diet, the emerging pattern is that the size range of utilized prey broadens with predator size and that relatively small prey are continuously included in the diet. Furthermore, the size of the coregonid prey was generally <15 cm, suggesting that coregonids up to this size are most vulnerable to predation and thus are inside the predation window of brown trout (Bohn et al. 2002; Kahilainen and Lehtonen 2003), which apparently is quite narrow.

To maximize foraging efficiency and growth, a predator should select the most abundant and available prey resources (i.e., Elliott and Hurley 2000). The prey fish density in the pelagic habitat was lowest in the single-morph whitefish lake (Lake 1) and increased markedly towards the vendace-dominated lake (Lake 5). In Lakes 2 and 3, DR whitefish dominated the pelagic habitat at medium densities (see also Kahilainen et al. 2004, 2005), whereas the highest pelagic prey densities were observed in the vendace-invaded Lakes 4 and 5. Our study showed that the ontogenetic shift to piscivory and the growth rate of brown trout during the first year in the lake was positively related to the abundance of pelagic prey fish and also demonstrated the energetic profitability of pelagic foraging of the piscivorous trout. The apparent profitability of selecting small-sized fish prey further suggests that the impact of such a piscivore feeding strategy may be greater than earlier assumed (Miller et al. 1988) and could have major effects on prey morphology (Brönmark and Miner 1992) and community structure (Hambright et al. 1991; Tonn and Paskowski 1992; Byström et al. 2003). Thus, high densities of small-sized prey, in particular vendace and DR whitefish, resulted in early shifts to piscivory, whereas low densities and higher growth rates of the available prey fish apparently delayed the ontogenetic shift to piscivory and reduced the predator growth.

In conclusion, our study demonstrates that brown trout is a habitat-, species-, and size-specific piscivore. The small-sized pelagic prey (DR whitefish and vendace) were consistently selected over the larger, benthic, coregonid morph. A weak, positive correlation was observed between predator and prey length, but the continuous inclusion of small prey suggests that this may represent favourable prey even for large predators. Brown trout furthermore switched to piscivory earlier and had a higher growth rate in lakes with small-sized pelagic prey present. In the absence of small-sized pelagic prey species like DR whitefish and vendace, the brown trout in contrast shifted to larger fish prey and apparently also to feeding in the littoral habitat. Hence, the brown trout is apparently also a flexible fish predator, being able to change feeding habitat and prey selection in accordance with the availability of suitable prey.

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Historical trends in productivity of 120 Pacific pink, chum, and sockeye salmon stocks reconstructed by using a Kalman filter

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Abstract: Temporal trends in productivity of Pacific salmon (*Oncorhynchus* spp.) stocks are important to detect in a timely and reliable manner to permit appropriate management responses. However, detecting such trends is difficult because observation error and natural variability in survival rates tend to obscure underlying trends. A Kalman filter estimation procedure has previously been shown to be effective in such situations. We used it on a Ricker spawner–recruit model to reconstruct indices of annual productivity (recruits per spawner (*R/S*) at low spawner abundance) based on historical data for 120 stocks of pink (*Oncorhynchus gorbuscha*), chum (*Oncorhynchus keta*), and sockeye (*Oncorhynchus nerka*) salmon. These stocks were from Washington, British Columbia, and Alaska. The resulting estimated temporal trends in productivity show large changes (on average 60%–70% differences in *R/S* and average ratios of highest to lowest *R/S* between 5.4 and 7.9 for the three species). Such changes suggest that salmon stock assessment methods should take into account possible nonstationarity. This step will help provide scientific advice to help managers to meet conservation and management objectives. The Kalman filter results also identified some stocks that did not share temporal trends with other stocks; these exceptions may require special monitoring and management efforts.

Résumé : Il est important de détecter les tendances temporelles de la productivité des stocks de saumons du Pacifique (*Oncorhynchus* spp.) au moment opportun et de façon fiable pour permettre des actions de gestion appropriées. Il est cependant difficile de détecter ces tendances, car les erreurs d'observation et la variation naturelle tendent à masquer les tendances sous-jacentes. On a montré antérieurement qu'une méthode d'estimation à filtre de Kalman peut être efficace dans de tels cas. Nous l'utilisons donc dans un modèle de reproducteurs–recrues de Ricker afin de reconstituer les indices de productivité annuelle (recrues par reproducteur (*R/S*) dans des conditions de faible abondance des recrues) d'après des données du passé sur 120 stocks de saumons roses (*Oncorhynchus gorbuscha*), kéta (*Oncorhynchus keta*) et rouges (*Oncorhynchus nerka*). Ces stocks proviennent de l'état de Washington, de la Colombie-Britannique et de l'Alaska. Les tendances temporelles estimées de la productivité que nous obtenons montrent d'importants changements (en moyenne, des différences de 60%–70% dans le nombre de *R/S* et des rapports moyens entre les *R/S* les plus élevés et les plus bas de 5,4 à 7,9 chez les trois espèces). De tels changements indiquent que les méthodes d'évaluation des stocks de saumons devraient tenir compte de ce que les population peuvent ne pas être stationnaires. Cette procédure servira à fournir des avis scientifiques aux gestionnaires afin de leur permettre de rencontrer leurs objectifs de conservation et de gestion. Les résultats au filtre de Kalman ont aussi identifié certains stocks qui ne partagent pas les mêmes tendances temporelles que les autres stocks; ces exceptions peuvent requérir des efforts particuliers de surveillance et de gestion.

[Traduit par la Rédaction]

Introduction

Objectives related to the management of Pacific salmon (*Oncorhynchus* spp.) on the west coast of North America often differ among fisheries managers, nongovernmental organizations, and harvesters. Nevertheless, these groups generally share a common interest in maintaining productive, abundant wild salmon stocks over the long term. There is thus a mutual desire to quickly and correctly detect changes in productivity and abundance over time, including both rapid changes to new persistent levels and gradual long-term trends. Management agencies also need to detect such changes so that appropriate action can be taken to prevent conservation crises when productivity is low or to reduce foregone economic and social benefits from fishing in periods when productivity is high. Furthermore, there is increasing interest in acting to help maintain biological diversity by preserving numerous small or less productive stocks of a given species, in case they might respond differently to environmental changes (e.g., Hilborn et al. 2003; Fisheries and Oceans Canada 2005).

Unfortunately, several factors complicate the task of reliably estimating time trends in salmon abundance (spawners or adult recruits) and productivity (recruits per spawner at

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low spawner abundance). For instance, large natural interannual variation tends to mask such trends. Furthermore, salmon data (especially for spawner abundance and in some cases catch as well) often contain unknown, but probably substantial, observation error that arises from several sources (e.g., bias and imprecision in sampling methods and in human perceptions). This combination of observation errors and high-frequency, year-to-year variation in salmon survival rates tends to make it difficult to detect true underlying changes in abundance or productivity.

New opportunities are emerging for dealing effectively with this challenge of reliably estimating temporal trends. In particular, the compilation of salmon and environmental data into large databases covering broad geographical areas has made investigations possible of large-scale patterns of variation in recruitment, catches, indices of survival rates, and also of potential environmental drivers of those changes. Such analyses have been aided by advanced statistical methods such as spatial correlation analysis (Pyper et al. 2001, 2002), principal components analysis (Hare et al. 1999), mixed-effects models (Myers et al. 1997), and hierarchical models that assume some shared components of variability (Mueter et al. 2002; Su et al. 2004). Evidence to date shows a tendency for positive correlations between time series of productivity indices for salmon stocks whose juveniles migrate to the ocean within several hundred kilometres of one another (Peterman et al. 1998; Botsford and Paulsen 2000; Pyper et al. 2005). This effect of distance suggests that these stocks share common physical and biological factors that influence their survival, particularly in the late freshwater and early marine periods. Knowledge of such shared variation among salmon stocks has helped to formulate hierarchical Bayesian models that improve estimates of productivity (Su et al. 2004).

Comparative analyses have also highlighted individual stocks that do not share temporal patterns and trends in productivity that are otherwise common throughout their region (e.g., Pyper et al. 2002). These stocks might be more likely than others to continue to respond differently to future natural and human influences. This type of divergent behavior may arise from differences in life history characteristics or localized habitat conditions, as well as human disturbances. One example of the benefit of maintaining of such biological diversity is the large, commercially valuable fisheries on Bristol Bay, Alaska, where sockeye salmon have maintained a lengthy persistence despite large changes in the stock composition of catch over the last three decades (Hilborn et al. 2003).

Here we use the Kalman filter (Kalman 1960) to provide a broad perspective on temporal patterns in productivity of sockeye (*Oncorhynchus nerka*), pink (*Oncorhynchus gorbuscha*), and chum (*Oncorhynchus keta*) salmon stocks. Unlike the methods of analysis mentioned above, the Kalman filter separately estimates systematic time trends from short-term, nonsystematic variability. Though it has been applied relatively little in ecology so far, the Kalman filter has nonetheless proven useful for a variety of ecological problems (Visser and Molenaar 1988; Pella 1993; Zeng et al. 1998). Stochastic computer simulations with known, user-defined, "true" underlying trends in productivity have previously shown the potential benefits of using a Kalman filter estimation procedure in conjunction with a Ricker stock–recruitment model (Peterman et al. 2000). Specifically, compared with the standard formulation and maximum-likelihood estimation of the Ricker model, Kalman filter estimation procedure can improve estimates of systematic underlying changes in mean productivity (i.e., the underlying temporal "signal") amid a large amount of nonsystematic, short-term variability (i.e., "noise", composed of both natural variability and observation error) (Peterman et al. 2000). When used for reconstructing temporal patterns of productivity from historical data for sockeye salmon in Bristol Bay, Alaska, the Kalman filter also revealed clearer underlying trends than indicated by standard Ricker model estimates of productivity (Peterman et al. 2003).

The ability of the Kalman filter to estimate systematic changes in productivity is relevant because some strategic salmon management questions deal with setting long-term goals or modifying harvest policies in the presence of overarching changes in factors such as habitat or climate. Such questions are different from short-term ones faced annually by managers, who need to determine the coming year's targets and regulations to achieve them. For the former, longer-term strategic questions, managers place higher priority on information about systematic temporal trends in productivity than on the high frequency noise of year-to-year variability. The properties of the Kalman filter noted above make this method well suited to such strategic management needs (Walters 1986; Peterman et al. 2000; Schnute and Kronlund 2002).

More specifically, our purpose was to apply the Kalman filter estimation procedure to examine temporal and spatial trends in productivity of salmon stocks of sockeye, pink, and chum from Washington, British Columbia (BC), and Alaska to address the following questions: (*i*) What are the spatial and temporal characteristics of historical productivity for salmon stocks in the study area? (*ii*) How do these patterns compare with those of the residuals from the standard Ricker model that assumes fixed parameters? (*iii*) Are there specific patterns or trends in productivity for specific stocks or groups of stocks that might indicate existing or potential future management opportunities or conservation concerns?

Materials and methods

Data

We used time series of age-specific abundance for spawners and adult recruits (catch plus escapement) for 120 wild stocks of Northeast Pacific salmon (Fig. 1), including pink salmon (Table 1; see also Pyper et al. 2001), chum salmon (Table 2; see also Pyper et al. 2002), and sockeye salmon (Table 3; see also Peterman et al. 1998; Pyper et al. 2005) (for complete data, see the Excel spreadsheet in the online supplementary material[4]). Data series were on average

[4] Supplementary data for this article are available on the journal Web site (cjfas.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 3793. For more information on obtaining material refer to cisti-icist.nrc-cnrc.gc.ca/cms/unpub_e.html.

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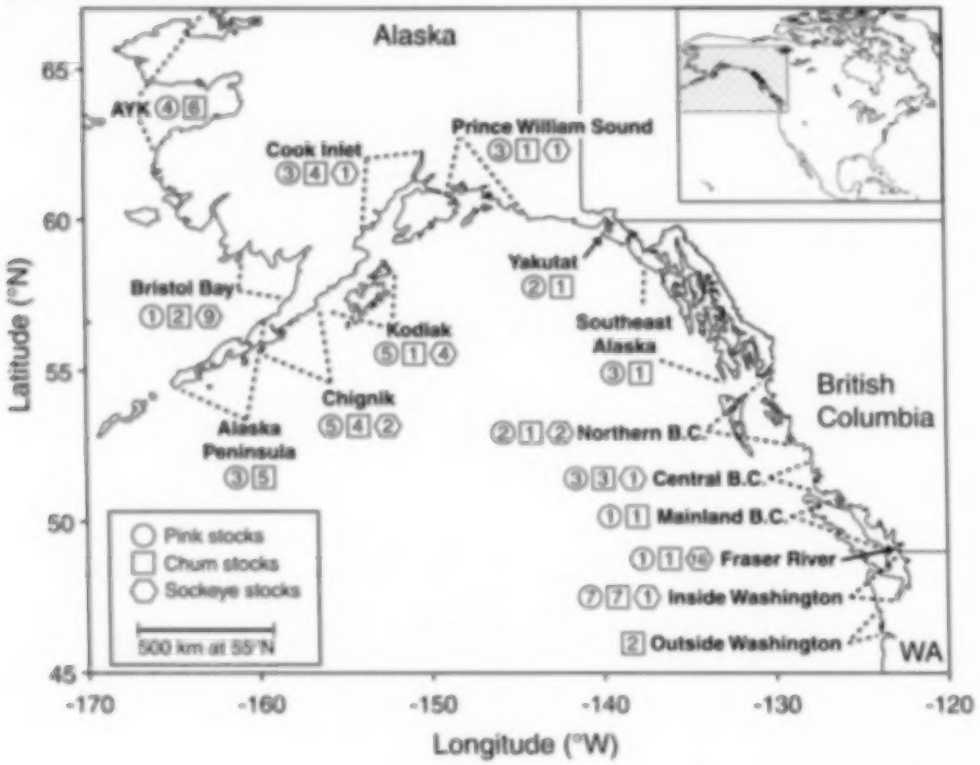
Fig. 1. Locations of the 120 wild stocks of pink (*Oncorhynchus gorbuscha*), chum (*Oncorhynchus keta*), and sockeye (*Oncorhynchus nerka*) salmon used to calculate indices of productivity from historical time series of spawner and recruitment data. The number of separate stock data sets in a named region is indicated by a number within each species-specific symbol (see legend). AYK is the Arctic–Yukon–Kuskokwim region. Figure is adapted from Pyper et al. (2005).



28 years long for pink salmon stocks (ranging from 15 to 47 years), 27 years for chum salmon stocks (ranging from 15 to 35 years), and 39 years for sockeye salmon stocks (ranging from 15 to 47 years). To explore similarities in productivity trends across space, we organized data on stocks by geographic region (Tables 1–3; Fig. 1). The regions were in most cases the areas used for management decisions. Where necessary, for each stock, we aggregated groups of spawners together to ensure that catch data could be allocated with confidence to that stock (Pyper et al. 2001, 2002, and 2005). For consistency in this paper, we use the term stock to represent such aggregates of fish (e.g., Kvichak River sockeye salmon) and to recognize that stocks are usually composed of multiple spawning populations. "Regions" here contain one or more stocks. Although pink salmon move through the same physical environment every other year, we separated pink salmon data into odd- and even-year runs because, with their fixed 2-year life cycle, they represent separate entities that may encounter different ecological conditions.

Indices of productivity

Throughout this paper, we used the Ricker model (Ricker 1975) as the basic stock–recruitment model:

$$(1) \quad \log_e(R_t/S_t) = a + bS_t + v_t$$

where S_t is abundance of spawners in brood year t, R_t is abundance of adult offspring from those spawners (i.e., adult recruits of all ages), a is the productivity (in units of $\log_e(R/S)$) at low spawner abundance (i.e., in the absence of density dependence), b reflects density-dependent effects, and v_t is a normally distributed error term with a mean of zero and variance σ_v^2.

From this starting point, we calculated two indices of change in salmon productivity. First, we fit the Ricker model to the entire spawner-recruitment time series for each stock using eq. 1; we then calculated the residuals. The time series of these residuals described year-to-year variability in productivity (in units of $\log_e(R/S)$) that is not explained by density-dependent effects of spawner abundance. These time series of Ricker residuals, scaled to a mean of zero and a standard deviation of one, constituted our first index of productivity.

Our second index was the annual a parameter value of a modified Ricker stock–recruitment model that was fit to the data using a Kalman filter estimation procedure. The strength of the Kalman filter lies in its ability to explicitly partition variation in $\log_e(R/S)$ into systematic trends over

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Table 1. Summary of data sets for 43 wild pink salmon (*Oncorhynchus gorbuscha*) stocks used to compute spawner-to-recruit survival rate indices.

						a_i				R/S		
Region	Stock or district	Brood year	Run	N	R	Mean	SD	Max.	Min.	Max.	Min.	Source[a]
Washington	Nooksack[b]	1959–1995	Odd	19	154	1.85	0	1.85	1.85	6.4	6.4	1
	Skagit[b]	1959–1995	Odd	19	889	1.58	0	1.58	1.58	4.8	4.8	1
	Stillaguamish[b]	1959–1995	Odd	19	293	1.08	0	1.08	1.08	3.0	3.0	1
	Snohomish[b]	1959–1995	Odd	19	258	1.28	0	1.28	1.28	3.6	3.6	1
	Puyallup River[b]	1959–1995	Odd	19	46	1.37	0.34	1.70	0.44	5.5	1.6	1
	Hood Canal[b,c]	1959–1995	Odd	19	135	0.71	0.30	1.22	0.21	3.4	1.2	1
	Dungeness[b]	1959–1995	Odd	19	88	0.77	0	0.77	0.77	2.2	2.2	1
BC south coast	Fraser River[b]	1957–1995	Odd	20	10815	1.62	0.08	1.69	1.47	5.4	4.4	2, 3
	South coast without Fraser River (statistical areas 12, 13, 15, 16)[d]	1954–1994	Even	21	2439	1.51	0	1.51	1.51	4.5	4.5	4, 5
BC central coast	Statistical area 10	1950–1995	Odd	23	32	1.25	0.17	1.39	0.84	4.0	2.3	6, 7
			Even	23	44	2.01	0.47	2.80	1.24	16.4	3.5	6, 7
	Statistical area 9	1950–1996	Odd	23	102	1.42	0.26	1.77	0.95	5.9	2.6	6, 7
			Even	24	409	1.72	0.29	2.12	1.26	8.3	3.5	6, 7
	Statistical area 8	1950–1996	Odd	23	1299	0.93	0	0.93	0.93	2.5	2.5	6, 7
			Even	24	4050	1.53	0	1.53	1.53	4.6	4.6	6, 7
BC north coast	Statistical area 6	1950–1995	Odd	23	1057	1.32	0.37	2.02	0.73	7.5	2.1	6, 7
			Even	23	2987	1.62	0	1.62	1.62	5.1	5.1	6, 7
	Statistical area 2E	1950–1995	Odd	23	49	0.84	0.57	1.73	–0.07	5.6	0.9	6, 7
			Even	23	838	1.43	0	1.43	1.43	4.2	4.2	6, 7
Southeast Alaska	Southern (districts 101–108)	1960–1996	Odd	18	29187	2.30	0.88	3.49	0.86	32.9	2.4	8
			Even	19	32379	1.69	0.30	2.41	1.29	11.1	3.6	8
	Northern inside (districts 109–112, 114, 115)	1960–1996	Odd	18	12446	1.52	0.37	2.03	0.87	7.6	2.4	8
			Even	19	12089	1.38	0.35	1.98	0.81	7.2	2.3	8
	Northern outside (district 113)	1960–1996	Odd	18	3996	0.84	0.06	0.94	0.75	2.6	2.1	8
			Even	19	2381	0.31	0	0.31	0.31	1.4	1.4	8
Yakutat	Situk River	1962–1990	Odd	13	227	1.57	0.25	1.83	1.12	6.2	3.1	8, 9
			Even	12	179	1.42	0.07	1.51	1.30	4.5	3.7	8, 9
	Humpy Creek	1972–1992	Odd	10	111	1.99	0.47	2.59	1.16	13.4	3.2	8, 9
			Even	11	47	1.43	0	1.43	1.43	4.2	4.2	8, 9
Prince William Sound	Eastern district	1967–1996	Odd	15	3474	1.65	0	1.65	1.65	5.2	5.2	10
			Even	15	3477	2.38	0.60	3.03	1.27	20.8	3.5	10
	Montague district	1971–1996	Odd	13	483	1.49	0.31	1.93	1.07	6.9	2.9	10
			Even	13	121	1.28	0.86	3.13	–0.53	22.9	0.6	10
	Southeastern district	1967–1996	Odd	15	1440	1.79	0.74	2.90	0.58	18.1	1.8	10
			Even	15	518	1.18	0.74	2.48	0.11	12.0	1.1	10

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Table 1 (*continued*).

Region	Stock or district	Brood year	Run	N	R	α_i				R/S		Source[a]
						Mean	SD	Max.	Min.	Max.	Min.	
Cook Inlet	Southern district[c]	1960–1996	Odd	18	246	1.03	0	1.03	1.03	2.8	2.8	11
			Even	19	146	1.17	0.35	1.76	0.62	5.8	1.9	11
	Outer district[c]	1960–1996	Odd	18	478	1.16	0	1.16	1.16	3.2	3.2	11
			Even	19	308	0.72	0	0.72	0.72	2.1	2.1	11
	Kamishak district[c]	1960–1996	Odd	16	180	0.98	0	0.98	0.98	2.7	2.7	11
			Even	18	200	0.84	0	0.84	0.84	2.3	2.3	11
Kodiak	Afognak district	1980–1996	Odd	8	1440	2.40	0.76	3.62	1.42	37.4	4.1	12
			Even	9	1245	2.58	0	2.58	2.58	13.2	13.2	12
	Westside district	1980–1996	Odd	8	6920	2.33	0.61	3.27	1.53	26.3	4.6	12
			Even	9	8208	2.35	0.18	2.60	2.10	13.5	8.2	12
	Alitak district	1980–1996	Odd	8	3448	2.38	0.58	3.21	1.60	24.9	5.0	12
			Even	9	1070	1.32	0.18	1.64	1.16	5.1	3.2	12
	Eastside–northend district	1980–1996	Odd	8	4430	1.91	0.54	2.64	1.23	14.0	3.4	12
			Even	9	1457	2.65	0	2.65	2.65	14.2	14.2	12
	Mainland district	1980–1996	Odd	8	1628	1.05	0	1.05	1.05	2.8	2.8	12
			Even	9	1178	0.95	0.47	1.81	0.28	6.1	1.3	12
Chignik	Chignik Bay district	1962–1995	Odd	15	88	2.71	1.18	4.78	1.31	118.9	3.7	13, 14
			Even	16	140	2.67	0.38	3.33	2.13	27.9	8.4	13, 14
	Central district	1962–1995	Odd	17	299	0.77	0	0.77	0.77	2.2	2.2	13, 14
			Even	17	191	1.51	0.41	2.05	0.96	7.8	2.6	13, 14
	Eastern district	1962–1995	Odd	17	357	0.72	0.23	1.11	0.39	3.0	1.5	13, 14
			Even	17	792	0.89	0	0.89	0.89	2.4	2.4	13, 14
	Western district	1962–1995	Odd	17	488	1.72	0.15	1.99	1.53	7.3	4.6	13, 14
			Even	17	428	2.64	0.01	2.65	2.62	14.1	13.7	13, 14
	Perryville district	1962–1995	Odd	17	464	1.09	0	1.09	1.09	3.0	3.0	13, 14
			Even	17	264	1.37	0	1.37	1.37	3.9	3.9	13, 14
Alaska Peninsula	Northwestern district	1962–1996	Odd	17	5	0.83	0	0.83	0.83	2.3	2.3	13, 15
			Even	18	112	0.99	0	0.99	0.99	2.7	2.7	13, 15
	Southeast and south-central districts	1962–1996	Odd	17	4790	1.65	0.44	2.26	1.03	9.6	2.8	13, 16
			Even	18	4084	2.04	0.55	2.68	1.20	14.6	3.3	13, 16
	Southwest and Unimak districts	1962–1996	Odd	17	1527	1.31	0.38	1.86	0.80	6.5	2.2	13, 16
			Even	18	2139	2.29	0.93	3.24	0.67	25.4	2.0	13, 16
Bristol Bay	Nushagak district[b]	1960–1996	Even	17	2673	1.17	0	1.17	1.17	3.2	3.2	17
Norton Sound	Nome	1978–1995	Odd	8	15	0.89	0	0.89	0.89	2.4	2.4	18, 19
			Even	9	575	1.21	0	1.21	1.21	3.3	3.3	18, 19
	Golovin	1968–1984	Odd	6	40	1.37	0	1.37	1.37	3.9	3.9	18, 19
			Even	9	222	1.35	0	1.35	1.35	3.9	3.9	18, 19
	Moses Point and Norton Bay	1968–1995	Odd	10	66	0.50	0	0.50	0.50	1.6	1.6	18, 19
			Even	12	494	1.47	1.02	2.90	−0.20	18.2	0.8	18, 19

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Table 1 *(concluded).*

Region	Stock or district	Brood year	Run	N	R	a_t			R/S			Source[a]
						Mean	SD	Max.	Min.	Max.	Min.	
	Unalakleet	1970–1995	Odd	10	52	1.81	0	1.81	1.81	6.1	6.1	18, 19
			Even	11	251	1.77	0	1.77	1.77	5.9	5.9	18, 19

Notes: Stocks are arranged from south to north, and data are shown separately for even- and odd-year runs. N is the number of brood years available; R is the average number of annual recruits (thousands); Mean a_t, SD a_t, Max. a_t, and Min. a_t give the average, standard deviation, maximum, and minimum, respectively, of the Kalman-filtered a_t time series. The maximum and minimum recruits/spawner (Max. and Min. R/S) are on the arithmetic scale and are derived from the maximum and minimum a_t values (i.e., $\exp(a_t)$).

[a]1, Jeff Haymes, Washington Department of Fish and Wildlife, 1111 Washington Street SE, Olympia, WA 98501, USA (personal communication); 2, Al Cass, Fisheries and Oceans Canada (DFO), 3190 Hammond Bay Road, Nanaimo, BC V9T 6N7, Canada (personal communication); 3, Jim Woodey, Pacific Salmon Commission, 600-1155 Robson Street, Vancouver, BC V6E 1B5, Canada (personal communication); 4, Clyde Murray, DFO, 3190 Hammond Bay Road, Nanaimo, BC V9T 6N7, Canada (personal communication); 5, Lia Bjesterveld, DFO, 200-401 Burrard Street, Vancouver, BC V6C 3S4, Canada (personal communication); 6, Dennis Rutherford, DFO, 3190 Hammond Bay Road, Nanaimo, BC V9T 6N7, Canada (personal communication); 7, Wood et al. (1999); 8, Tim Zadina, Alaska Department of Fish and Game (ADF&G), 2030 Sealevel Drive, Suite 205, Ketchikan, AK 99901, USA (personal communication); 9, Clark (1995); 10, Mark Willette, ADF&G, P.O. Box 669, Cordova, AK 99574-0669, USA (personal communication); 11, Ted Otis, ADF&G, 3298 Douglas Place, Homer, AK 99603-8027, USA (personal communication); 12, Kevin Brennan, ADF&G, 211 Mission Road, Kodiak, AK 99615-6399, USA (personal communication); 13, Denby Lloyd, ADF&G, 211 Mission Road, Kodiak, AK 99615-6399, USA (personal communication); 14, Owen and Sarafin (1999); 15, Murphy et al. (1999); 16, Campbell et al. (1999); 17, Michael Link, ADF&G, 333 Raspberry Road, Anchorage, AK 99518-1599, USA (personal communication); 18, Betsy Brennan, ADF&G, 333 Raspberry Road, Anchorage, AK 99518-1599, USA (personal communication); 19, Brennan et al. (1998).

[b]Data were only available for odd years (e.g., brood years 1959, 1961, ..., 1995), because few if any pink salmon spawn in even years.

[c]Sum of Dosewallips, Duckabush, and Hamma Hamma data sets.

[d]Only even-year data were used for the Mainland BC data set, because catches in most odd years were confounded by catch of Fraser River pink salmon.

[e]Sum of Humpy Creek, Port Graham, and Seldovia Bay data sets.

[f]Sum of Port Chatham, Port Dick, Rocky River, and Windy Creek data sets.

[g]Sum of Brown's Peak Creek, Bruin River, and Sunday Creek data sets.

[h]Data were only available for even years, because few if any pink salmon spawn in odd years.

time in productivity and random sources of variation that are independent of those trends. To accomplish this, the Kalman filter requires: (*i*) an observation equation (Chatfield 1989), which in this case is a description of the underlying biological relationship between spawners and recruits, and (*ii*) a system or transition equation (Chatfield 1989), in this case, a description of how one of the parameters of that biological model changes over time. More specifically, the observation equation was adapted from the basic Ricker model (eq. 1) by assuming a time-varying a parameter:

$$(2) \qquad \log_e(R_t/S_t) = a_t + bS_t + v_t$$

This time-varying a_t was our second index of productivity.

The transition equation for the Kalman filter in our case must describe the expected temporal variation in a_t, but the true underlying pattern of this variation is unknown. However, previous simulation work (Peterman et al. 2000) indicates that a random-walk model can track a wide variety of hypothetical temporal trends in a_t, including a step function, a sine wave, and an autoregressive lag-1 (AR(1)) process. The Kalman filter with a random-walk model for a_t therefore can be expected to effectively attribute appropriate portions of the observed variation in the data to either the systematic time trends in a_t or to short-term variation under a range of natural productivity patterns as well. Other forms of the transition equation (e.g., AR(1), ARIMA: autoregressive integrated moving average) generally do not fit the same data that we used here as well as the random-walk model does (B.J. Pyper, Cramer Fish Sciences, 600 NW Fariss Road, Gresham, Oregon, USA, personal communication). Therefore, we chose that random-walk model for a:

$$(3) \qquad a_t = a_{t-1} + w_t$$

with error terms v_t and w_t in eqs. 2 and 3 assumed to be normally distributed and independent, with means of zero and variances σ_v^2 and σ_w^2, respectively.

While it is possible to have either the a or b parameter (or both) vary over time, we limited our analysis to a time-varying a_t for three reasons. First, Adkison et al. (1996) found that for Bristol Bay sockeye stocks, the a parameter tended to change much more over time than the b parameter. Second, assuming that the Ricker b parameter (but not a) was time-varying would imply that substantial changes in $\log_e(R/S)$ would occur only when spawner abundance was large (i.e., a change in the level of density-dependent feedback). However, a changing a_t parameter reflects the more likely situation that environmental processes influence survival rates of a stock to a similar proportional degree regardless of spawner abundance. Third, based on values of the small-sample AIC_c (Akaike information criterion), models with only a time-varying a_t fit data for our 120 salmon stocks better than models either with a time-varying b_t or with both parameters time-varying (B.J. Pyper, Cramer Fish Sciences, 600 NW Fariss Road, Gresham, Oregon, USA, personal communication).

The Kalman filter recursively estimated a_t each year, using a Bayesian approach that weighted the prior expectation for a_t estimated from previous years against the evidence of the data for year t. In the resulting time series of "filtered" (Harvey 1989) annual a_t estimates, each a_t depended only on data up

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Table 2. Summary of 40 wild chum salmon (*Oncorhynchus keta*) data sets used to compute spawner-to-recruit indices of survival rate.

					α				*R*/*S*		
Region	Stock or district	Brood year	*N*	*R*	Mean	SD	Max.	Min.	Max.	Min.	Source[a]
Washington west coast	Willapa Bay	1968–1993	26	60	1.05	0	1.05	1.05	2.9	2.9	1
	Grays Harbour	1969–1993	21	46	1.03	0.03	1.07	0.97	2.9	2.6	1
Puget Sound	Skagit River	1968–1993	26	125	0.77	0	0.77	0.77	2.2	2.2	2
	Nooksack–Samish rivers	1968–1993	26	65	1.43	0.30	1.80	0.80	6.0	2.2	2
	Stillaguamish–Snohomish rivers	1968–1993	26	124	0.99	0.16	1.19	0.70	3.3	2.0	2
	Hood Canal	1968–1993	26	163	2.27	0.39	2.85	1.69	17.4	5.4	2
	South Sound fall	1968–1993	26	256	2.02	0.11	2.17	1.87	8.8	6.5	2
	South Sound summer	1968–1993	26	40	1.41	0.40	1.95	0.73	7.0	2.1	2
	South Sound winter	1968–1993	26	54	1.59	0	1.59	1.59	4.9	4.9	2
BC south coast	Fraser	1959–1992	34	886	0.99	0	0.99	0.99	2.7	2.7	3
	Inner south coast without Fraser River	1959–1992	34	1188	1.16	0.14	1.33	0.90	3.8	2.5	3
BC central coast	Statistical area 10	1960–1995	36	45	1.60	0.69	3.11	–0.44	22.5	0.6	4
	Statistical area 9	1960–1995	36	60	1.32	0.10	1.45	1.13	4.3	3.1	4
	Statistical area 8	1960–1994	35	488	1.94	0.11	2.12	1.80	8.3	6.0	4
BC north coast	Statistical area 6	1965–1992	28	307	1.32	0	1.32	1.32	3.7	3.7	5
Southeast Alaska	Kadashan River	1969–1984	16	55	1.75	0.61	2.78	1.02	16.2	2.8	6
Yakutat	East Alsek River[b]	1960–1987	21	25	1.60	0	1.60	1.60	4.9	4.9	7
Prince William Sound	Total	1966–1993	28	790	1.88	0.70	2.95	0.63	19.0	1.9	8
Cook Inlet	Outer district[c]	1964–1994	31	40	1.07	0.51	2.16	0.34	8.6	1.4	9
	Southern district[d]	1964–1994	29	20	1.56	0.92	3.68	0.34	39.8	1.4	9
	Kamishak district[e]	1964–1994	25	115	1.41	0.33	1.77	0.95	5.9	2.6	9
	Upper Cook Inlet	1972–1993	22	1505	1.10	0.36	1.59	0.61	4.9	1.8	10
Kodiak	Total	1962–1992	31	1296	2.06	0.34	2.66	1.26	14.3	3.5	11
Chignik	Central district	1962–1992	31	62	1.62	0.74	3.03	0.45	20.6	1.6	12, 13
	Eastern district	1962–1992	31	143	1.44	0.72	3.01	–0.46	20.4	0.6	12, 13
	Western district	1962–1992	31	118	2.04	0	2.04	2.04	7.7	7.7	12, 13
	Perryville district	1962–1992	31	64	1.33	0.52	2.43	0.60	11.3	1.8	12, 13
Alaska Peninsula	Northern district	1962–1994	33	279	1.39	0.65	2.70	–0.35	14.8	0.7	12, 14
	Izembek–Moffet	1962–1994	33	228	0.96	0.34	1.61	0.28	5.0	1.3	12, 14
	Bechevin–Swanson	1962–1994	33	69	1.44	0.69	2.73	0.09	15.4	1.1	12, 14
	Southeast district and south-central districts	1962–1994	33	700	1.76	0.48	2.38	0.74	10.8	2.1	12, 15
	Southwest district and Unimak districts	1962–1994	33	379	2.03	0.71	3.08	0.54	21.7	1.7	12, 15
Bristol Bay	Nushagak River	1974–1993	18	727	1.28	0.44	1.88	0.33	6.6	1.4	16
	Togiak River	1978–1992	15	438	2.13	0.14	2.31	1.91	10.1	6.8	16
AYK[g] and Norton Sound	Yukon River Fall[f]	1974–1995	22	843	0.89	0.46	1.41	–0.36	4.1	0.7	17, 18
	Anvik River	1972–1993	22	1042	1.09	0	1.09	1.09	3.0	3.0	17, 19
	Andreafsky River	1972–1995	24	276	0.81	0.46	1.48	–0.36	4.4	0.7	17, 20
	Kwiniuk and Tubutulik rivers	1965–1995	31	69	1.16	0.36	1.62	0.47	5.1	1.6	17, 21

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Table 2 (*concluded*).

Region	Stock or district	Brood year	N	R	a_t			R/S		Source[a]
					Mean	SD	Max.	Min.	Max.	Min.	
	Norton Sound district 1	1975–1995	21	55	1.34	0.46	2.19	0.20	9.0	1.2	17, 22
	Kotzebue Sound	1962–1979	18	378	2.48	0.51	3.02	1.55	20.5	4.7	23

Notes: Stocks are arranged from south to north. N is the number of brood years available; R is the average number of annual recruits (thousands); Mean a_t, SD a_t, Max. a_t, and Min. a_t give the average, standard deviation, maximum, and minimum, respectively, of the Kalman-filtered a_t time series. The maximum and minimum recruits/spawner (Max. and Min. R/S) are on the arithmetic scale and are derived from the maximum and minimum a_t values (i.e., $\exp(a_t)$).

[a] 1. Rick Brix and John Linth, Washington Department of Fish and Wildlife (WDFW), 48 Devonshire Road, Montesano, WA 98563, USA (personal communication); 2. Jeff Haymes, WDFW, 1111 Washington Street SE, Olympia, WA 98563, USA (personal communication); 3. Ryall et al. (1999); 4. Ron Gerak, Fisheries and Oceans Canada (DFO), 417–2nd Avenue West, Prince Rupert, BC V8J 1G8, Canada (personal communication); 5. Les Juntz, DFO, 417–2nd Avenue West, Prince Rupert, BC V8J 1G8, Canada (personal communication); 6. Ben Van Alen, Alaska Department of Fish and Game (ADFG), 802–3rd Street, Douglas, AK 99824-0020, USA (personal communication); 7. Tim Zadina, ADFG, 2030 Sea Level Drive, Ketchikan, AK 99901, USA (personal communication); 8. Mark Willette, ADFG, 43961 Kalifornsky Bch Road, Soldotna, AK 99669-8367, USA (personal communication); 9. Ted Otis, ADFG, 3298 Douglas Place, Homer, AK 99603-8027, USA (personal communication); 10. Ken Tarbox, ADFG, 43961 Kalifornsky Bch Road, Soldotna, AK 99669-8367, USA (personal communication); 11. Kevin Brennan, ADFG, 211 Mission Road, Kodiak, AK 99615-6399, USA (personal communication); 12. Debby Lloyd, ADFG, 211 Mission Road, Kodiak, AK 99615-6399, USA (personal communication); 13. Owen and Sarafin (1999); 14. Murphy et al. (1999); 15. Campbell et al. (1999); 16. Michael Link, ADFG, 333 Raspberry Road, Anchorage, AK 99518-1599, USA (personal communication); 17. Doug Eggers, ADFG, 1255 W. 8th Street, Juneau, AK 99811-5526, USA (personal communication); 18. Eggers (2001); 19. Clark and Sandone (2001); 20. Clark (2001*b*); 21. Clark (2001*c*); 22. Clark (2001*d*); 23. Bigler (1985).

[b] Spawner abundances for East Alsek River were used as an index of escapement; catch data were total harvests in districts 181 through 189.

[c] Sum of Port Graham and Dogfish Lagoon data sets.

[d] Sum of Port Dick and Rocky River data sets.

[e] Sum of Bruin, McNeil, and Big and Little Kamishak rivers, Ursus Cove and Lagoon, and Cottonwood Creek – Iniskin River data sets.

[f] Sum of fall-run chum salmon for Tanana River, Yukon River mainstem, and Yukon River tributary data sets.

[g] Artic–Yukon–Kuskokwim.

through year t. We subsequently applied fixed-interval smoothing to the filtered estimates (Visser and Molenaar 1988). This smoothing process begins with the most recent filtered a_t value and works backward through time, computing a weighted average of the filtered estimate for time t and the smoothed estimate for time $t + 1$ at each step (Peterman et al. 2003). The smoothed a_t values thus take into account not only the information provided by the data up to year t, but also the information from year t onward. This smoothing process produces the minimum-variance unbiased estimates of a_t, as well as the maximum likelihood estimates (Fraser and Potter 1969). All results and discussions of a_t estimates below refer to these smoothed a_t values. To facilitate comparisons among the various stocks' a_t estimates that were reconstructed by the Kalman filter and also between those values and standardized Ricker residuals for the same stock, we standardized a_t values for each stock to a mean of zero and standard deviation of one. To examine the level of concordance between estimates of productivity (i.e., a_t) and abundance (i.e., estimates of recruitment and spawner abundance), we also calculated for several key stocks of interest the standardized recruitment and spawner abundance estimates with a mean of zero and a standard deviation of one.

The b parameter and variance terms σ_v and σ_w were assumed constant over time and were estimated using maximum likelihood. The exact procedures for our Kalman filter estimation method are described in Peterman et al. (2003), and its implementation in S-PLUS (Insightful Corporation, Seattle, Washington) code is available in the online supplementary material (NRC Data Depository[4]). Additional details for this general method are found in Meinhold and Singpurwalla (1983), Harvey (1989), and Zeng et al. (1998).

Correlation analysis

We compared correlations across stocks to quantify the extent to which variation in the a_t index of productivity is shared among salmon stocks. Specifically, we examined spatial covariation among productivities of stocks by calculating pairwise Pearson product–moment correlation coefficients between time series of Ricker residuals. We also calculated such correlations for the time series of a_t values reconstructed using the Kalman filter. We excluded from this analysis any pair of stocks for which one or both time series of estimated a_t were constant over time, as was sometimes the case for Kalman filter reconstructions. Such cases arose when the Kalman filter attributed all variance in the data to random sources of error, as opposed to systematic process variation. Pairs of time series were also excluded if they had fewer than 10 brood years in common. We tested correlation coefficients (r) for significance with H_0: $r = 0$ using a modification of the method described by Chelton (1994) to account for the effect of serial autocorrelation (Pyper and Peterman 1998*a*, 1998*b*). All tests for statistical significance were two-tailed, using $\alpha = 0.05$. We emphasize, though, that we were most interested in the general patterns of correlations among many salmon stocks, rather than the statistical significance of particular pairwise comparisons.

To provide a concise overview of key results of this analysis and to facilitate comparison with earlier studies, we also computed average correlations among groups of salmon

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Table 3. Summary of 37 wild sockeye salmon (*Oncorhynchus nerka*) data sets used to compute spawner-to-recruit indices of survival rate.

					a_c				*R*/*S*		
Region	Stock or district	Brood year	*N*	*R*	Mean	SD	Max.	Min.	Max.	Min.	Source[a]
Puget Sound	Lake Washington	1967–1993	27	274	0.62	0	0.62	0.62	1.9	1.9	1
Fraser early Stuart	Early Stuart	1950–1996	47	340	1.35	0.48	2.36	0.47	10.6	1.6	1
Fraser early summer run	Bowron	1950–1996	47	45	1.65	0.10	1.76	1.47	5.8	4.3	1
	Gates	1952–1996	45	46	1.38	0	1.38	1.38	4.0	4.0	1
	Nadina	1950–1996	47	68	1.68	0.18	2.01	1.26	7.5	3.5	1
	Pitt	1950–1996	47	72	1.59	0.40	2.28	0.88	9.8	2.4	1
	Raft	1950–1996	47	28	1.31	0.20	1.73	0.95	5.7	2.6	1
	Seymour	1950–1996	47	138	1.51	0.28	1.80	0.91	6.0	2.5	1
Fraser summer run	Chilko	1950–1996	47	1533	2.13	0.12	2.33	1.98	10.3	7.2	1
	Horsefly	1950–1996	47	1322	1.29	0.36	1.95	0.84	7.1	2.3	1
	Late Stuart	1950–1996	47	585	1.70	0	1.70	1.70	5.5	5.5	1
	Stellako	1950–1996	47	499	1.95	0	1.95	1.95	7.1	7.1	1
Fraser Birkenhead	Birkenhead	1950–1996	47	424	2.29	0.42	2.95	1.22	19.0	3.4	1
Fraser late run	Adams	1950–1996	47	2026	1.54	0.09	1.63	1.37	5.1	3.9	1
	Cultus	1950–1996	47	67	1.38	0.09	1.56	1.28	4.7	3.6	1
	Portage	1951–1996	43	45	1.84	0.35	2.26	1.14	9.6	3.1	1
	Weaver	1950–1996	47	289	1.96	0.34	2.27	1.34	9.7	3.8	1
BC central coast	Long Lake	1980–1994	15	350	0.38	1.12	1.73	−2.06	5.6	0.1	2
BC north coast	Skeena	1950–1994	45	2056	0.82	0.13	0.98	0.55	2.7	1.7	2
	Nass	1967–1991	25	650	1.72	0.34	2.45	1.35	11.6	3.8	3
Prince William Sound	Copper	1961–1993	33	1435	2.11	0.36	2.81	1.52	16.6	4.6	4
Cook Inlet	Cook	1968–1992	25	4770	1.64	0.12	1.84	1.46	6.3	4.3	5
Kodiak	Ayakulik	1965–1993	29	574	0.89	0.28	1.30	0.28	3.7	1.3	6
	Frazer	1965–1993	29	409	1.86	0.46	2.53	1.18	12.6	3.3	6
	Early Upper Station	1969–1993	25	104	0.94	0.21	1.16	0.43	3.2	1.5	6
	Late Upper Station	1970–1993	24	539	1.33	0.39	2.18	0.72	8.8	2.1	6
Chignik	Black	1950–1993	44	1028	1.58	0.27	1.90	1.13	6.7	3.1	6
	Chignik	1950–1993	44	960	1.89	0.30	2.24	1.42	9.4	4.1	6
Bristol Bay	Branch	1956–1995	40	499	1.12	0.14	1.31	0.93	3.7	2.5	7
	Egegik	1956–1995	40	6424	1.85	0.61	2.88	0.91	17.8	2.5	7
	Igushik	1956–1995	40	965	1.58	0.73	2.92	0.17	18.5	1.2	7
	Kvichak	1956–1995	40	12450	0.55	0.64	1.77	−0.97	5.9	0.4	7
	Naknek	1956–1995	40	3487	1.37	0.08	1.47	1.23	4.3	3.4	7
	Nuyakuk	1956–1982	27	932	1.39	0.30	1.81	0.95	6.1	2.6	7
	Togiak	1956–1995	40	518	1.79	0.15	2.02	1.53	7.5	4.6	7

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Table 3 (*concluded*).

Region	Stock or district	Brood year	N	R	a_i			*RS*			Source[a]
					Mean	SD	Max.	Min.	Max.	Min.	
	Ugashik	1956–1995	40	2729	1.35	0.94	2.90	–0.40	18.3	0.7	7
	Wood	1956–1995	40	2715	1.54	0.36	2.21	1.03	9.1	2.8	7

Note: Stocks are arranged from south to north. N is the number of brood years available; R is the average number of annual recruits (thousands); Mean a_i, SD a_i, Max. a_i, and Min. a_i give the average, standard deviation, maximum, and minimum, respectively, of the Kalman-filtered a_i time series. The maximum and minimum recruits/spawner (Max. and Min. *RS*) are on the arithmetic scale and are derived from the maximum and minimum a_i values (i.e., $\exp(a_i)$).

[a]1, Jim Woodey and Mike Lapointe, Pacific Salmon Commission, 600–1155 Robson Street, Vancouver, BC V6E 1B5, Canada (personal communication); 2, Chris Wood, Fisheries and Oceans Canada (DFO), 3190 Hammond Bay Road, Nanaimo, BC V9T 6N7, Canada (personal communication); 3, Les Jantz, DFO, 417-2nd Avenue West, Prince Rupert, BC V8J 1G8, Canada (personal communication); 4, Mark Willette, Alaska Department of Fish and Game (ADF&G, 4396) Kalifornsky Bch Road, Soldotna, AK 99669-8367, USA (personal communication); 5, Ken Tarbox, ADF&G, 4396) Kalifornsky Bch Road, Soldotna, AK 99669-8367, USA (personal communication); 6, Patricia Nelson, ADF&G, 211 Mission Road, Kodiak, AK 99615-6399, USA (personal communication); 7, Michael Link, ADF&G, 333 Raspberry Road, Anchorage, AK 99518-1599, USA (personal communication).

stocks for larger geographic regions. These regions correspond to those used in Pyper et al. (2001, 2002, 2005) and reflect a mixture of natural geographic boundaries and management jurisdictions.

In addition to formal correlation analysis, we show time series plots of reconstructed a_i because simple correlation values between complete time series do not fully describe particular trends during certain time periods, reversals of direction of trends, or other features relevant to conservation and management. Because our main focus in this paper is on changes in productivity across time within salmon stocks and on comparisons among stocks, we primarily refer in the Results section to the compact dot plots of standardized productivity index values shown in Figs. 2–4. For readers interested in actual rather than standardized values of productivity indices, we provide graphs of original, unscaled, smoothed Kalman filter a_i time series as online supplementary material (Supplementary Figs. S1–S4, available from the NRC Data Depository[4]).

Results

Kalman filter reconstructions of a_i identified many clear underlying temporal trends in productivity of all three salmon species (right-hand columns of Figs. 2–4 in standard deviation units). For instance, the pink salmon stocks of the Alaska Peninsula and Chignik show increasing trends in a_i from about 1970 through the 1990s (Fig. 2). This right-hand column shows large open circles (values between 1 and 2 standard deviations below the respective stock-specific means) during the 1960s and early 1970s, shrinking in size over time until they become small solid dots (near-mean values), and then becoming increasingly large solid dots (between 1 and 2 standard deviations above the respective stock-specific means during the 1980s and 1990s). The Kalman filter extracted such long-term temporal trends that were obscured by large short-term variability in the noisier index of productivity based on Ricker residuals (compare left and right columns of Figs. 2–4). These Kalman filter time series are considerably smoother than the Ricker residuals, because the Kalman filter suppresses much of the random (i.e., nonsystematic), short-term variability and emphasizes the underlying time trends in mean productivity, whereas the Ricker residuals reflect all variation in the stock–recruitment data, both random, short-term variability as well as long-term trends. Many changes in productivity estimated by the Kalman filter were monotonic (e.g., Alaska Peninsula and most Chignik pink salmon; Fig. 2), whereas others were nonmonotonic trends (e.g., Bristol Bay and Fraser River sockeye salmon; Fig. 4). Some of those changes occurred over only a few years, but others occurred across decades. It is notable that periods of unusually high or low a_i values often persisted for at least 5 years. In some cases, all variability in the time series of stock–recruitment data was interpreted by the Kalman filter as high-frequency variation not related to systematic trends, resulting in constant smoothed a_i values without any time trend (e.g., the series of equally small dots in Fig. 2 for most Washington pink salmon stocks).

On average, the variance due to the temporal trend (σ_w^2) was smaller than the remaining variation not related to that

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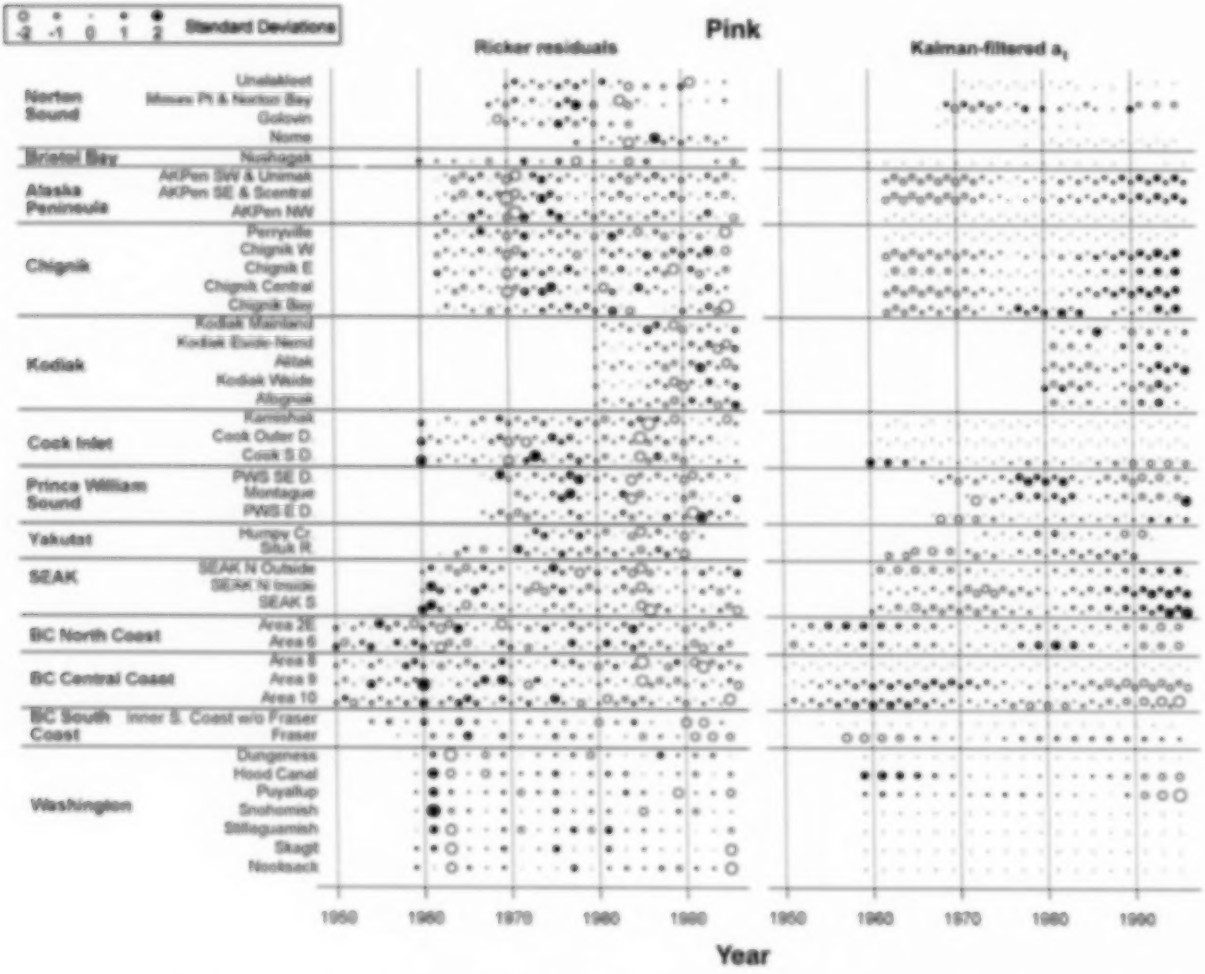
Fig. 2. Pink salmon (*Oncorhynchus gorbuscha*) time series of Ricker residuals (left) and a_t values produced by Kalman filter estimation (right) by brood year (year when the group of fish was spawned). Even-year runs and odd-year runs were analyzed separately. For ease of comparison, results for even-year runs are shown vertically offset slightly below results for odd-year runs. Stocks are arranged from south (bottom of figure) to north (top of figure). Time series are in standard deviation units (i.e., scaled to a mean of zero and a standard deviation of one); scale is at top left. Solid circles represent above-average values; open circles represent below-average values. The radius of circles represents the magnitude (absolute value) of indices (i.e., large solid circles represent years with very high values, whereas large open circles represent years with very low values). Zero (or near-zero) values are shown as small dots to distinguish them from years with missing values.



trend (σ_w^2); the ratio of (average σ_w^2 / average σ_r^2) was 0.26 for pink salmon, 0.34 for sockeye salmon, and 0.61 for chum salmon. Thus, the slowly changing trend was an important part of the total variation. This relative magnitude of the variances differed widely among stocks; those stocks that had a large range in productivity over time had a ratio of between 0.4 and 0.7. This ratio provided no new information beyond what is shown in Figs. 2–4, because it tended to be similar within species and within regions, just like similarities in productivity trends shown in those figures.

From the standpoint of conservation and management, many of the changes in a_t were extremely large and important. Recall that the a_t parameter is equivalent to the average logarithm of recruits per spawner at extremely low spawner abundance (eq. 2). Thus, to put the changes in a_t into perspective, we converted each a_t value to the equivalent recruits per spawner (*R*/*S*, using e^{a_t}) (Tables 1–3, second- and third-to-last columns). Then, for each stock, we calculated the difference between the highest and lowest *R*/*S* in the time series as a percentage of the highest *R*/*S*. Across the stocks that showed a time-varying a_t, the average of these percentages for each species was unexpectedly large and was also surprisingly consistent across species: 66% for even-year pink salmon, 60% for odd-year pink salmon, 70% for chum salmon, and 60% for sockeye salmon. These large changes in productivity were also reflected by the average of stock-specific ratios of the highest to the lowest *R*/*S* over the course of a given time series. The average ratios were

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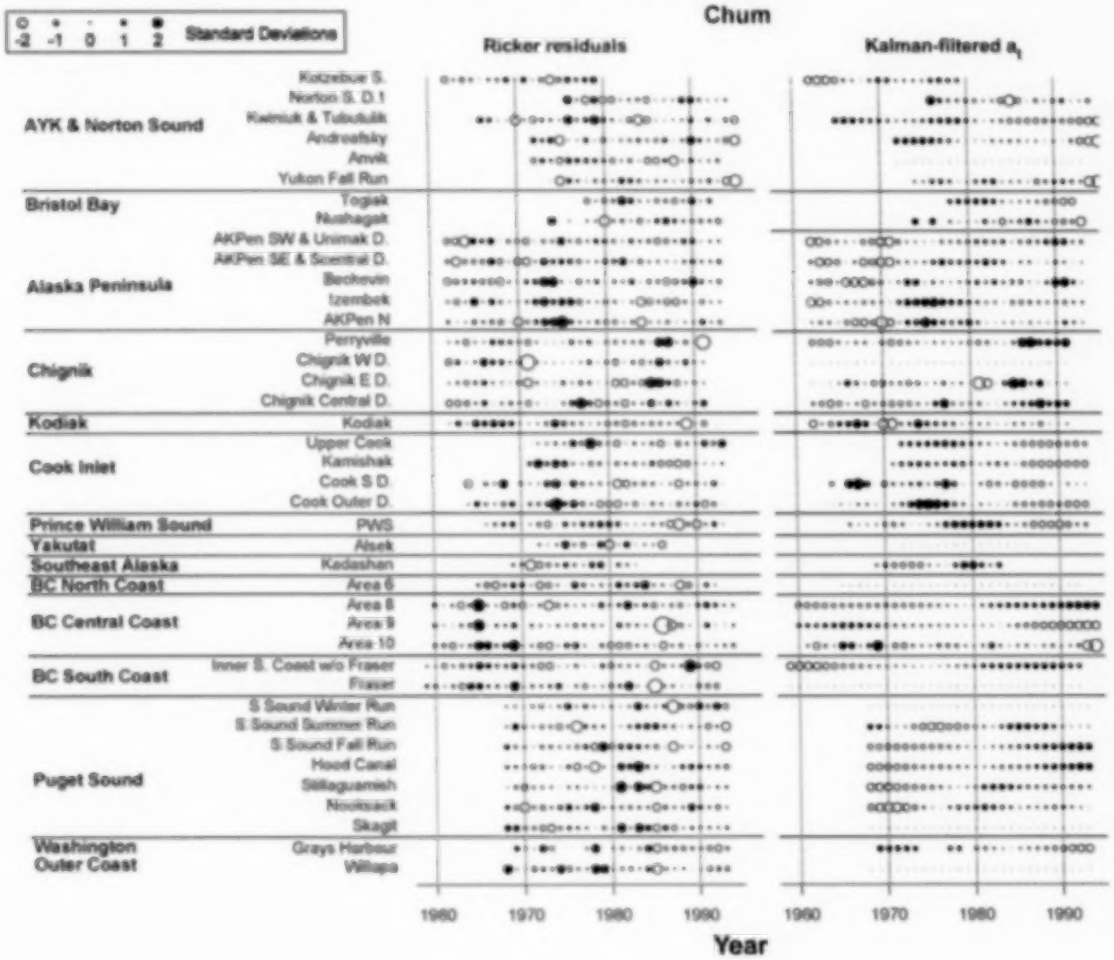
Fig. 3. Chum salmon (*Oncorhynchus keta*) time series of Ricker residuals (left) and a_i values produced by Kalman filter estimation (right) by brood year (year when the group of fish was spawned). Stocks are arranged from south (bottom of figure) to north (top of figure). Time series are in standard deviation units (i.e., scaled to a mean of zero and a standard deviation of one); scale is at top left. Solid circles represent above-average values; open circles represent below-average values. The radius of circles represents the magnitude (absolute value) of indices (i.e., large solid circles represent years with very high values, whereas large open circles represent years with very low values). Zero (or near-zero) values are shown as small dots to distinguish them from years with missing values.



7.1 for even-year pink salmon, 5.4 for odd-year pink salmon, 7.9 for chum salmon, and 5.6 for sockeye salmon. Some of these ratios of the maximum to minimum *R/S* were particularly large, as exemplified by ratios of 35 for chum salmon in statistical area 10, 39 for even-year pink salmon in the Montague district, and 44 for sockeye salmon from Long Lake. Such large values for changes in *R/S* have important implications for management and conservation (see Discussion section). We found no consistent patterns in these percentage differences or ratios of *R/S* between and within regions or between and within species. This lack of patterns was due to the wide range of values commonly found among stocks within each species and within each region (Tables 1–3).

The Kalman filter results also illustrate three other important points. First, the a_i series were typically positively correlated for stocks of a given species within the same geographic region (Table 4 and diagonal cells of Figs. 5*a*–5*d*). Second, in most cases, we found that within-region correlations for a_i series were stronger than correlations for Ricker residuals (Table 4). In some cases, such as within Alaska Peninsula pink salmon and Chignik sockeye salmon, virtually identical patterns in smoothed a_i for stocks in each area resulted in within-region correlations close to 1.0. Third, comparisons of a_i series among regions within species showed mostly positive correlations within Alaska ("northern area": top-right block of cells bordered by broken lines in Figs. 5*a*–5*d*) and within BC–Washington ("southern area": lower-left block of cells), but predominantly negative correlations between these areas (Fig. 5, lower-right block).

Despite the general coherence of temporal patterns of a_i

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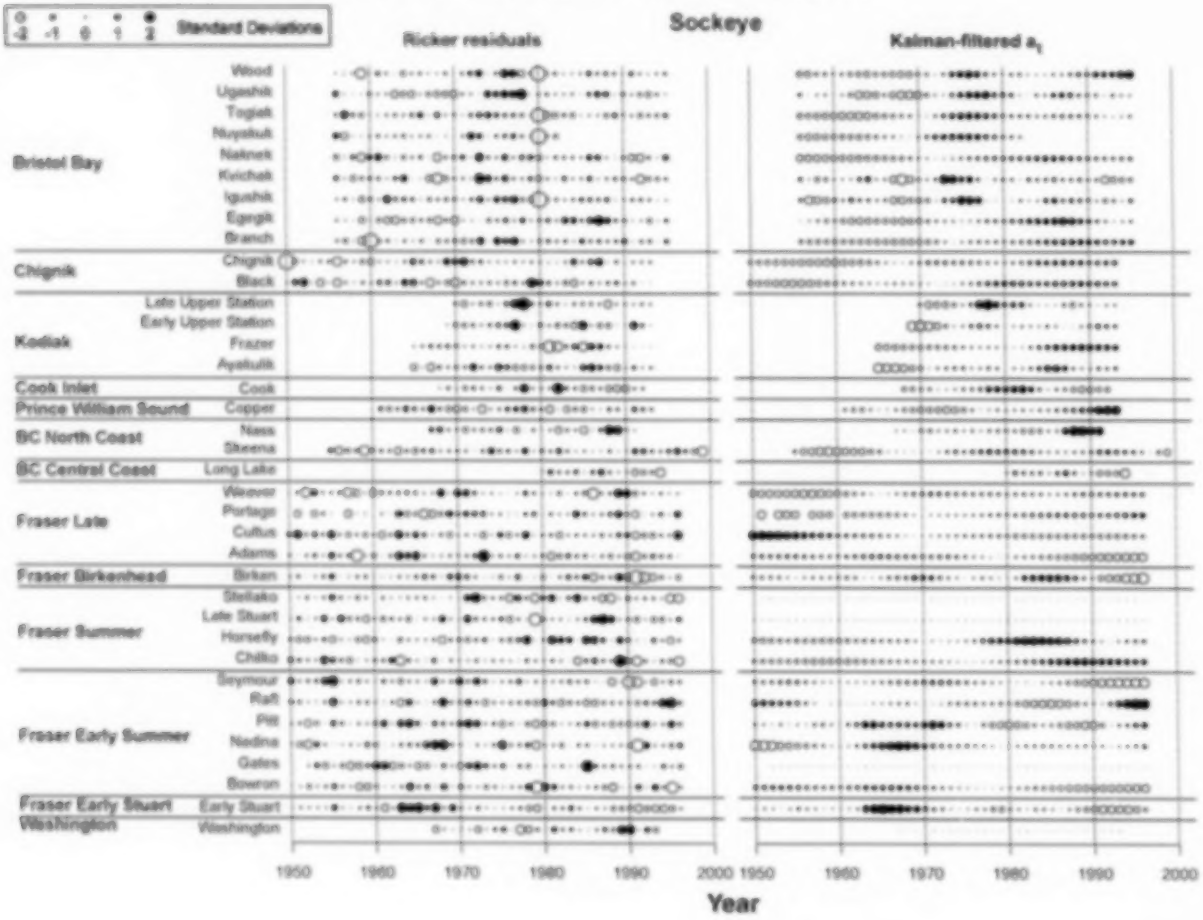
Fig. 4. Sockeye salmon (*Oncorhynchus nerka*) time series of Ricker residuals (left) and a_t values produced by Kalman filter estimation (right) by brood year (year when the group of fish was spawned). Stocks are arranged from south (bottom of figure) to north (top of figure). Time series are in standard deviation units (i.e., scaled to a mean of zero and a standard deviation of one); scale is at top left. Solid circles represent above-average values; open circles represent below-average values. The radius of circles represents the magnitude (absolute value) of indices (i.e., large solid circles represent years with very high values, whereas large open circles represent years with very low values). Zero (or near-zero) values are shown as small dots to distinguish them from years with missing values.



within species and regions (Table 4), high and low productivities often occurred at different times for different stocks within a region (Figs. 2–4). For example, temporal trends were out of phase to various degrees among chum salmon stocks in Puget Sound and also in the Alaska Peninsula regions (Fig. 3), as well as among Kodiak sockeye stocks (Fig. 4).

While the Kalman filter analysis thus identified shared, positively correlated long-term trends in productivity among salmon stocks, not all short-term variability quantified in the process of Kalman filtering was necessarily due to observation error or purely local factors. Examples of short-term fluctuations that affected stocks across large geographical areas include (*i*) the rapid change from high to low productivity between 1961 and 1963 brood year Washington pink salmon (left side of Fig. 2), (*ii*) extremely low productivity during the mid-1980s for pink salmon stocks from the BC central coast up through Cook Inlet, (*iii*) the episode of unusually high productivity experienced by 1965 brood year chum salmon throughout BC (left side of Fig. 3), and (*iv*) the very low productivity experienced by several stocks of 1980 brood year Bristol Bay sockeye salmon (left side of Fig. 4). None of these short-term variations in Ricker residuals appears clearly in the a_t signals. This lack of sensitivity of the Kalman filter to such spatially-correlated short-term variation is also apparent in the analysis of within-region correlations (Table 4). In the case of the BC central coast chum salmon and Fraser late-run sockeye salmon, for example, the stocks in each of those regions shared similar patterns of short-term variation, but differed with respect to longer-term patterns (Figs. 3 and 4), which resulted in a positive correlation for Ricker residuals, but negative correlation for Kalman a_t series (Table 4). The opposite was the case for the Chignik sockeye salmon (Fig. 4), where diver-

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Table 4. Average within-region correlations for pairs of stock-specific time series of Ricker residuals and also for Kalman filter reconstructions of Ricker a_i time series.

Region	Ricker residuals	Kalman-filtered a_i
Even-year pink salmon		
BC central coast	0.41	0.75
BC north coast	0.56	—
Southeast Alaska	0.23	0.84
Yakutat	0.30	—
Prince William Sound	0.61	0.53
Cook Inlet	0.57	—
Chignik	0.53	0.79
Alaska Peninsula	0.59	0.99
Norton Sound	0.47	—
Odd-year pink salmon		
Puget Sound	0.49	—
Washington	0.81	—
BC central coast	0.20	0.89
BC north coast	0.02	0.14
Southeast Alaska	0.58	0.82
Prince William Sound	0.50	0.95
Cook Inlet	0.36	—
Chignik	0.42	0.78
Alaska Peninsula	0.75	1.00
Chum salmon		
Washington west coast	0.81	—
Puget Sound	0.31	0.60
BC south coast	0.51	—
BC central coast	0.41	–0.25
Cook Inlet	0.36	0.68
Chignik	0.47	0.60
Alaska Peninsula	0.49	0.54
Bristol Bay	0.09	0.22
Norton Sound and Kotzebue	0.33	0.45
Sockeye salmon		
Fraser early summer	0.20	0.26
Fraser summer	0.18	0.72
Fraser late	0.19	–0.27
BC north coast	0.45	—
Kodiak	–0.04	0.34
Chignik	–0.12	0.88
Bristol Bay	0.35	0.62

Note: We only show regions that had two or more series with at least 10 valid data years. Because series with constant a_i values had to be excluded from correlation analyses, within-region correlations for Kalman a_i could not be calculated for some regions.

gent short-term patterns in the Ricker residuals (correlation of –0.12) masked the strong positive correlation (0.88) between long-term trends identified by the a_i series.

In the remainder of this section, we describe the a_i time trends in more detail. The purpose is not to convey fine points of individual stocks' timing and direction of changes in productivity, but rather to illustrate general points about similarities among stocks, regions, and species, as well as differences among them. Unless stated otherwise, "productivity" henceforth refers only to a_i values.

Pink salmon a_i time series

Pink salmon show a range of patterns. For the majority of northern (i.e., Alaskan) pink stocks, Kalman filter a_i values were low during the 1960s, followed in most cases by a steady increasing trend that continued through to the 1990s (Fig. 2). In contrast, productivities for southern (i.e., Washington and BC) stocks were generally moderate or high during the 1960s but then declined during the 1970s, a trend that continued into the 1990s for the majority of these stocks. For many pink stocks in the northern and a few in the southern regions, an increase in a_i values in the 1970s was the only other distinct change in long-term dynamics. Some pink stocks experienced another major reversal, declining from above-average to below-average values through the 1980s. As might be expected, patterns for odd- and even-year runs of the same stock were mostly similar (Fig. 2). However, there were some exceptions, the most notable being odd- and even-year runs of Kodiak, Prince William Sound eastern district, Cook Inlet southern district, and BC north coast stocks.

Similarities in a_i time series of pink salmon stocks produced strong positive correlations within certain regions that contained more than one stock (thick-lined diagonal cells in Figs. 5*a*, 5*b*). Pairwise correlations were also predominantly positive among Alaskan pink stocks. In contrast, correlations between Alaskan and BC–Washington pink stocks (both even- and odd-year runs) were predominantly negative, although mixed in sign for odd-year pink salmon (Figs. 5*a*, 5*b*). For example, a_i series for odd-year pink salmon from Washington and the central and north coast of BC were mostly negatively correlated with a_i series for southeast Alaskan odd-year pink salmon (average correlation –0.69, ranging from –0.06 to –0.97; Fig. 5*b*).

Chum salmon a_i time series

Like a_i patterns for pink salmon, patterns for chum salmon were generally consistent within regions (Fig. 3); correlations within regions were mostly positive (diagonal in Fig. 5*c*). However, patterns across larger geographical areas were more variable than those for pink salmon, especially for the southern part of the study area. Although negative correlations predominate, there is considerable variability in the magnitudes and signs of correlations among southern chum stocks and among correlations between southern and northern chum stocks (Fig. 5*c*).

As with the pink salmon stocks, the late 1960s and early 1970s covered a period of very low productivity for about half the chum salmon stocks, followed by increases during the mid- to late 1970s (Fig. 3). Most southern chum stocks continued to increase in productivity into the 1990s, a trend shared by Alaskan, but not BC–Washington, pink stocks.

There were some positive between-species correlations in a_i patterns for Alaskan pink and chum salmon within regions (diagonal cells of Figs. 6*a*, 6*b*) and between nearby regions such as Chignik and the Alaska Peninsula (top right of Figs. 6*a*, 6*b*). For other Alaskan regions though, most correlations between pink and chum stocks were negative because Alaskan pink productivity was mostly stable or increasing after the mid-1970s, whereas productivity for Alaskan chum stocks in the Arctic–Yukon–Kuskokwim (AYK), Bristol Bay, Kodiak, and Cook Inlet regions

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Fig. 5. Matrix of pairwise correlations between stock-specific, Kalman-filtered a_y time series for (*a*) even-year pink (*Oncorhynchus gorbuscha*), (*b*) odd-year pink, (*c*) chum (*Oncorhynchus keta*), and (*d*) sockeye (*Oncorhynchus nerka*) salmon. Within a given region, a row (or a column) of circles represents results for a given salmon stock. Thick solid lines delineate within-region correlations along the diagonal. Broken lines separate Alaskan stocks from those in Washington and British Columbia. Positive correlation coefficients are shown as solid circles; negative coefficients are shown as open circles. The radius of circles represents the strength of the correlation. Correlation coefficients that are not significantly different from zero at the $\alpha = 0.05$ level are shown in gray rather than black shading. Some columns or rows are empty (indicating that data exist, but fewer than 10 data points exist for the correlation analysis) or missing (indicating that there are no such stocks in the region; e.g., even-year Washington pink salmon).

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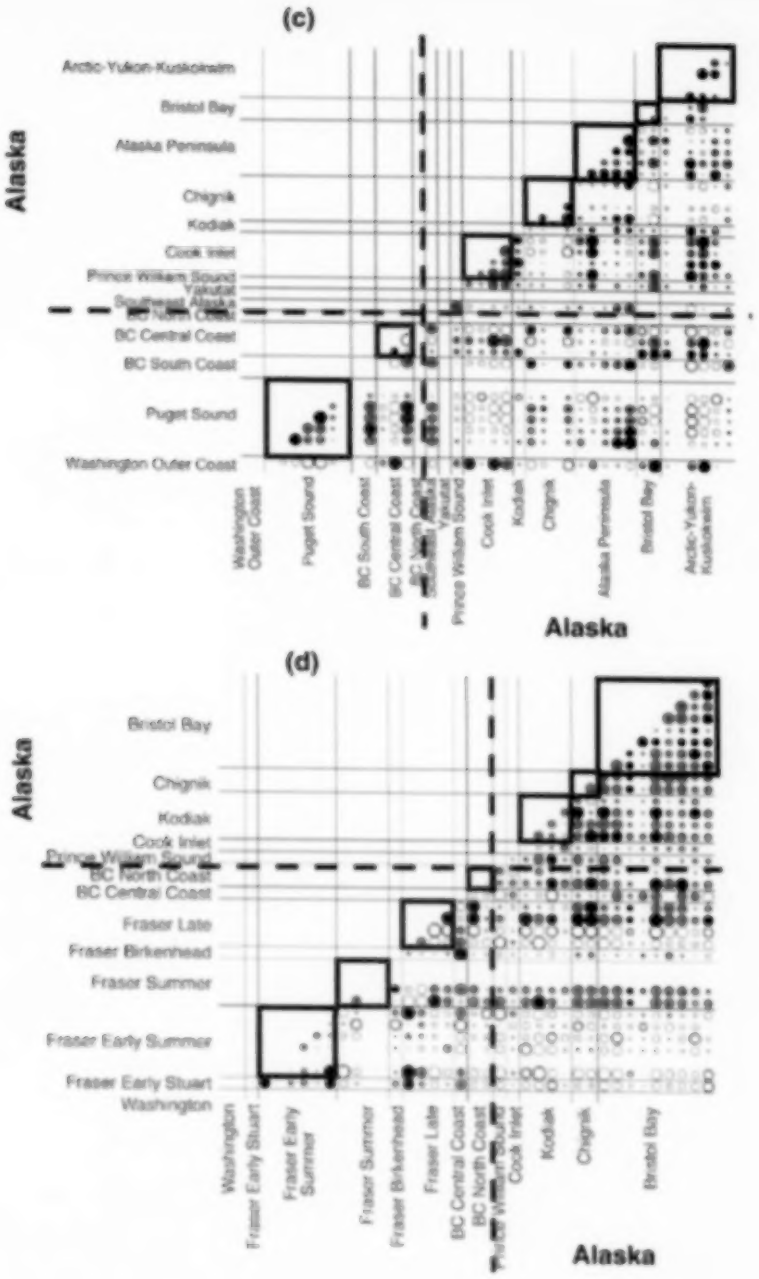
Fig. 5. (*concluded*).



decreased during that period (Figs. 2, 3). One notable exception to such negative between-region correlations is the strong positive correlation between Puget Sound chum salmon and Alaskan pink salmon, mainly due to increased productivity in both groups after the mid-1970s (top left block of Figs. 6*a*, 6*b*).

Sockeye salmon a_i time series

Time trends in a_i for sockeye salmon were also similar within regions and among certain regions (Figs. 4 and 5*d*). Correlations in productivities between pairs of northern (i.e., Alaskan) sockeye stocks were typically strong and almost universally positive (upper right of Fig. 5*d*), whereas

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Fig. 6. Cross-species correlations between (*a*) chum salmon (*Oncorhynchus keta*) and even-year pink salmon (*Oncorhynchus gorbuscha*) stocks, (*b*) chum salmon and odd-year pink salmon stocks, (*c*) sockeye salmon (*Oncorhynchus nerka*) and even-year pink salmon stocks, (*d*) sockeye salmon and odd-year pink salmon stocks, and (*e*) chum salmon and sockeye salmon stocks. Thick-lined rectangles outline results for between-species comparisons within the same region. Positive correlation coefficients are shown as solid circles; negative coefficients are shown as open circles. The radius of circles represents the strength of the correlation. Correlation coefficients that are not significantly different from zero at the $\alpha = 0.05$ level are shown in gray rather than black shading. Some columns or rows are empty (indicating that data exist, but fewer than 10 data points exist for the correlation analysis) or missing (indicating that there are no such stocks in the region).

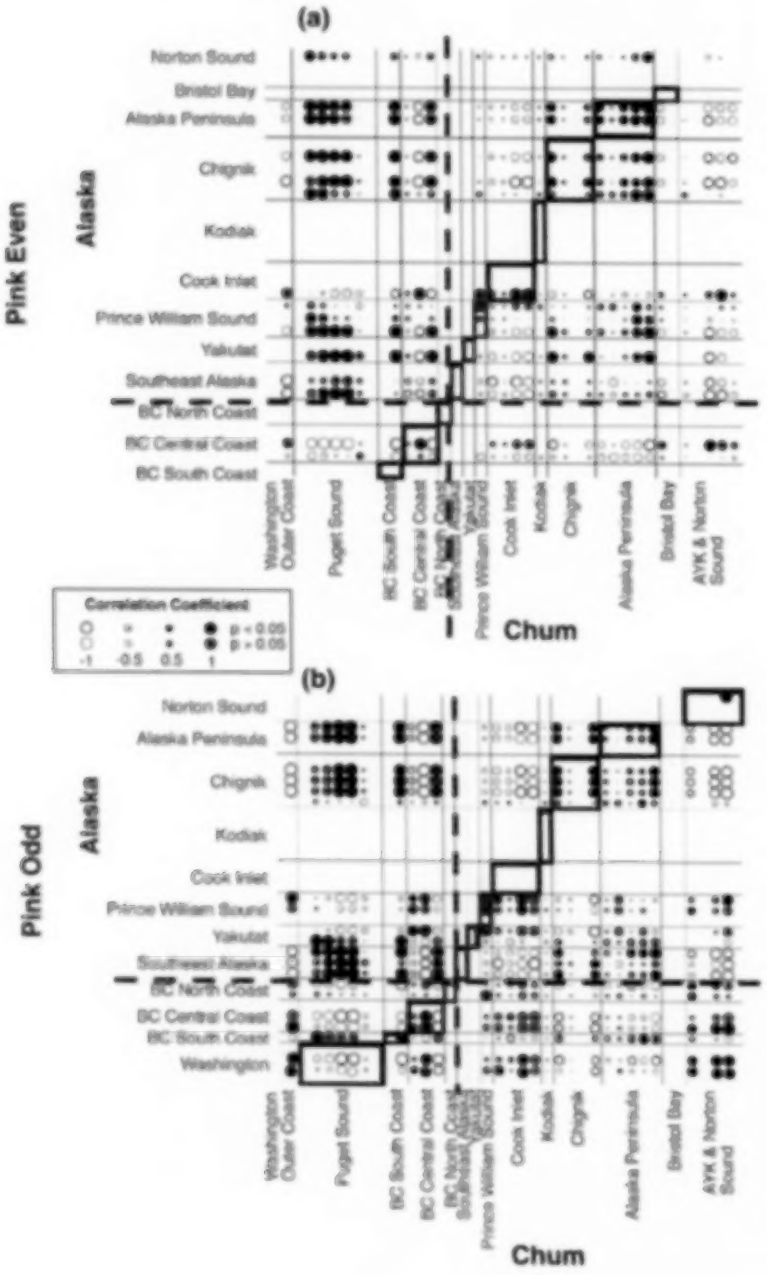

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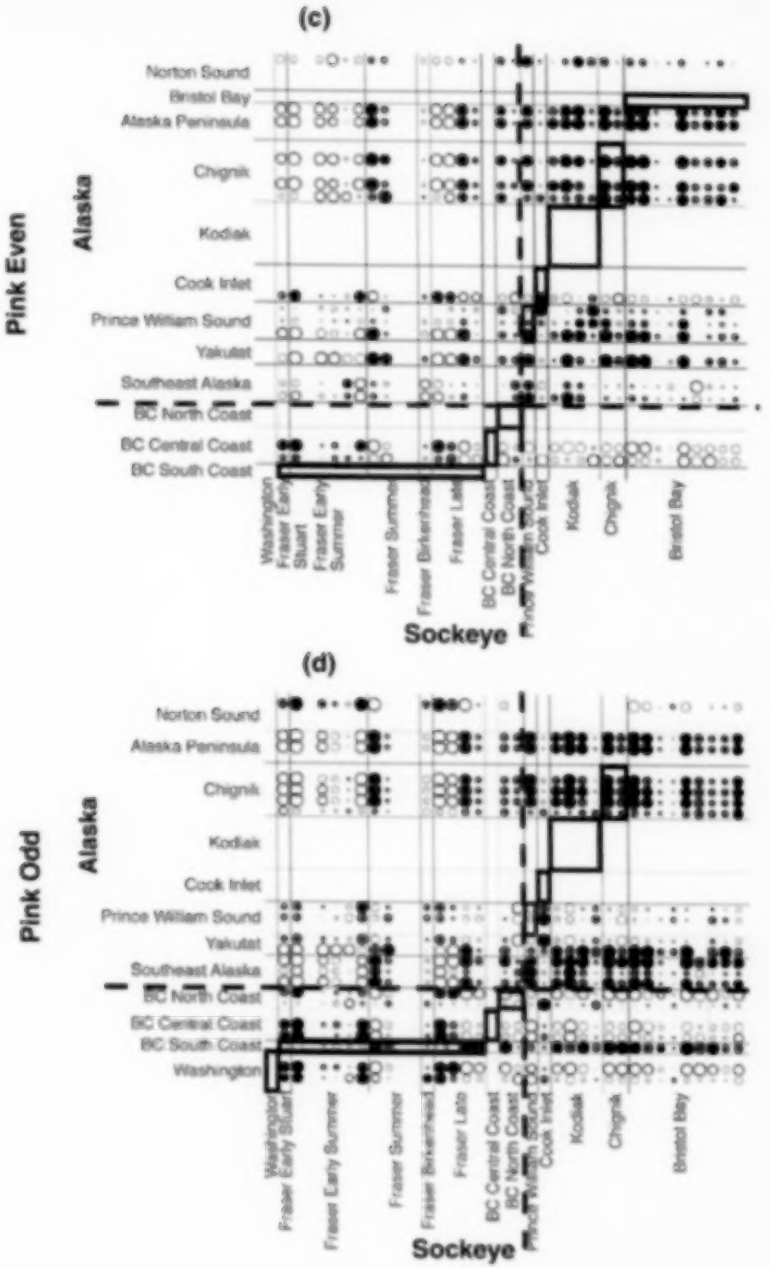
Fig. 6. (*continued*).



correlations between northern and southern sockeye stocks were quite variable but negative correlations predominated (lower right of Fig. 5*d*).

One key exception to the general within-area coherence was the group of Fraser River sockeye salmon stocks, which showed quite diverse temporal patterns (Fig. 4). Correlations among productivities of pairs of Fraser River stocks tended to be weak and were often negative (lower left of Fig. 5*d*). There was little consistency in either long- or short-term patterns for Fraser River sockeye as a whole or within the run-timing groups (e.g., early summer, summer, or late runs).

Like northern pink salmon and chum salmon stocks, northern sockeye salmon stocks generally experienced a period of below-average a_t during the 1960s, followed by sharp increases in a_t over the next decade or so (Fig. 4). These similarities resulted in predominantly positive between-species correlations between northern sockeye and

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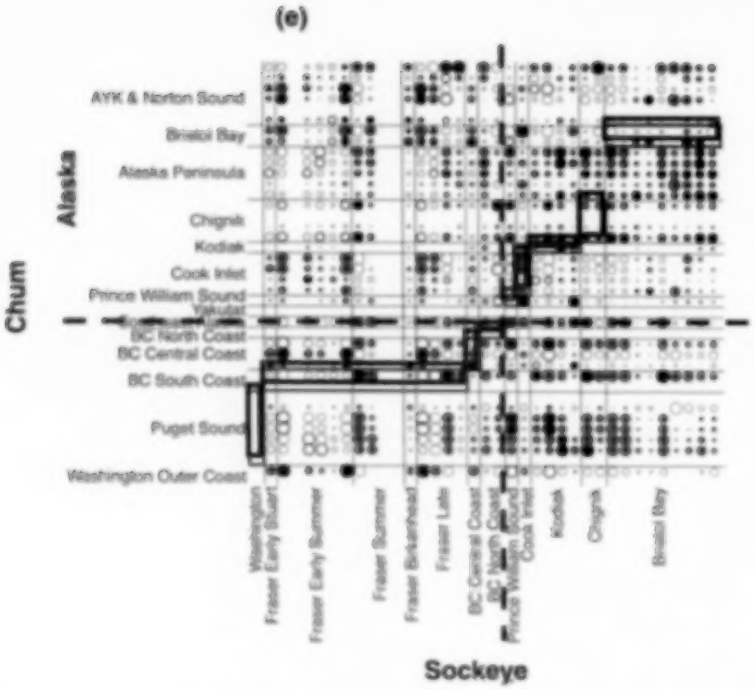
Fig. 6. (*concluded*).



northern pink and chum stocks, although the correlations with chum salmon were weaker (upper right of Figs. 6*c*, 6*d*, 6*e*). Patterns for sockeye were not as well synchronized as those for pink salmon though, and for Alaskan stocks, productivity typically began to increase for sockeye and chum a few years earlier than for pink salmon (Figs. 2–4). Correlations between BC and Alaska pink and sockeye salmon, though, were primarily negative.

A closer look at the relationship among recent productivity trends, abundance of recruits, and spawning escapement (Fig. 7) illustrates the implications of nonstationary productivity patterns and also highlights management opportunities and challenges arising from these patterns. For example, several stocks in the study area experienced a substantial increase in productivity through the early 1990s, yet not all cases showed similar increases in recruitment (Fig. 7). Conditional upon sufficient recruitment and low harvest rates, such increases in productivity can quickly restore abundance of spawners after low periods, as has been the case, for example, for Pitt and Raft sockeye after 1990. High productivity also creates potential for increased harvest levels, although the substantial increase in spawner abundance for the majority of stocks in Fig. 7 indicates that harvesting did not take full advantage of the increase in productivity, possibly because higher priority was placed on rebuilding spawning stocks. Because the evidence from the Kalman filter analysis suggests that temporal trends in productivity often persist for at least half a decade, such reconstructions of recent productivity trends may help to guide harvesting capacity away from stocks that are in a low-productivity phase.

At the other extreme, stocks that have experienced a strong decline in productivity in recent years pose a major management concern (Fig. 8). Such a decline in productivity in the 1990s was most evident for several pink salmon stocks from Washington and BC, chum salmon stocks from the BC central coast and the AYK region, and sockeye salmon stocks from the Fraser River and BC central coast (Fig. 8). In all these cases, the continued decline in productivity eventually resulted in declining recruitment, in spite of mostly average escapement (or, in the case of Andreafsky, Kwiniuk and Tubutulik chum, above-average escapement; Fig. 8). It thus appears that for the stocks shown in Fig. 8, management actions were often adequate to constrain the fishery and maintain spawning escapement at or near historical levels, but it is also clear that those escapement levels were not high enough to reduce the impact of declining productivity sufficiently to maintain abundance of recruits. Kalman filter analysis might help detect such persistent downward trends in productivity early enough to implement a proactive management regime and perhaps prevent a substantial decline in adult recruits.

Discussion

The Kalman filter results document considerable temporal variation in productivity of pink, chum, and sockeye salmon stocks on the west coast of North America. We re-emphasize that in this paper, we are mainly concerned with productivity (reflecting recruits per spawner), not simply abundance. Some variation in productivity was shared among stocks, whereas other stocks showed distinctive patterns. In most cases, the systematic changes in productivity reflected by Kalman filter a_t values were substantial, resulting in large

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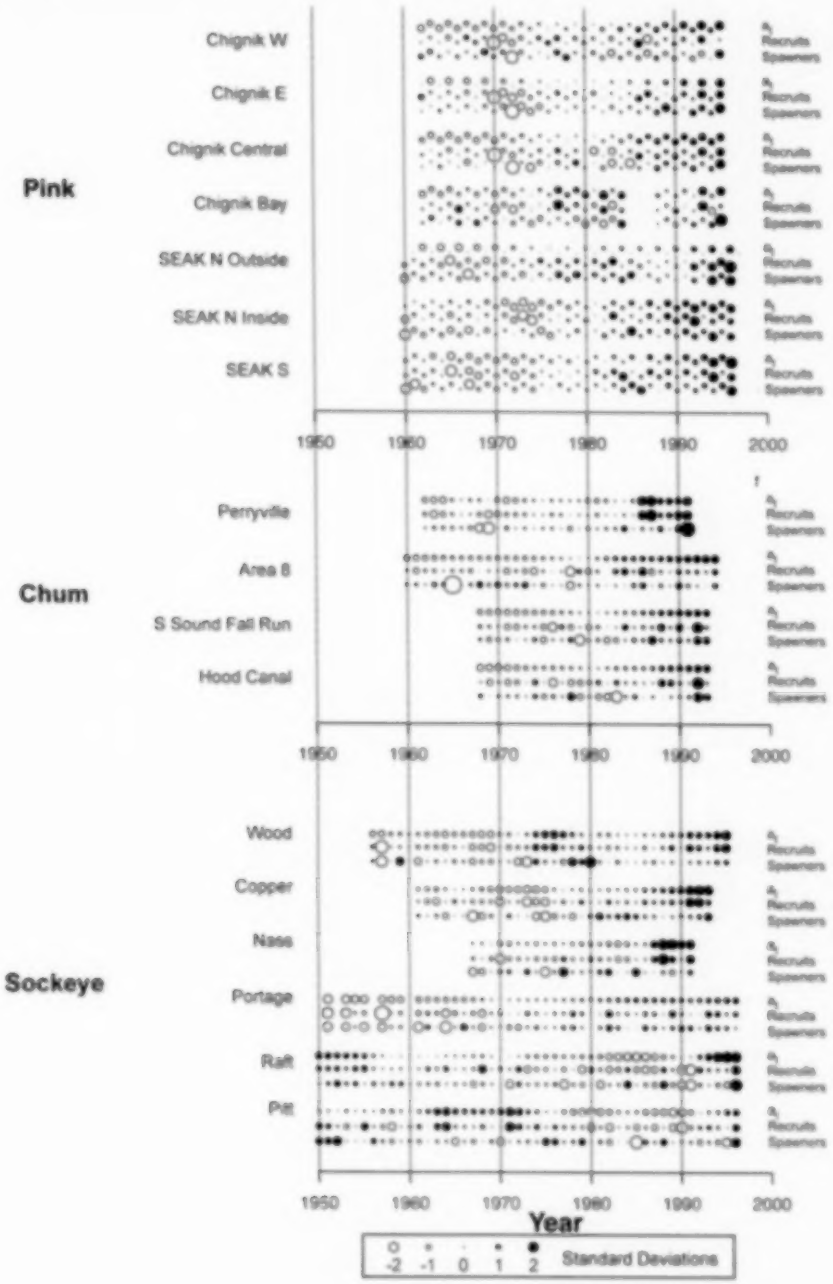
Fig. 7. Kalman-filtered a_t time series, recruitment, and spawner abundance for some stocks with high and (or) increasing productivity in the 1990s. Like the Kalman-filtered a_t time series, spawner and recruit time series are scaled to a mean of zero and a standard deviation of one to highlight common patterns.



average differences between the highest and lowest recruits per spawner during the time series. Those changes occurred at various rates, from slow in some stocks to rapid in others and highly variable in still others. Recall that the variation indicated by the Kalman-filter-estimated a_t values describes systematic trends or changes to persistent new levels of productivity, as opposed to short-term, year-to-year variation in recruits per spawner. This distinction is important because the systematic trends mainly affect long-term policies and planning, estimation of conservation concerns, and evaluation of success of past management actions. In contrast, short-term variation is obviously also

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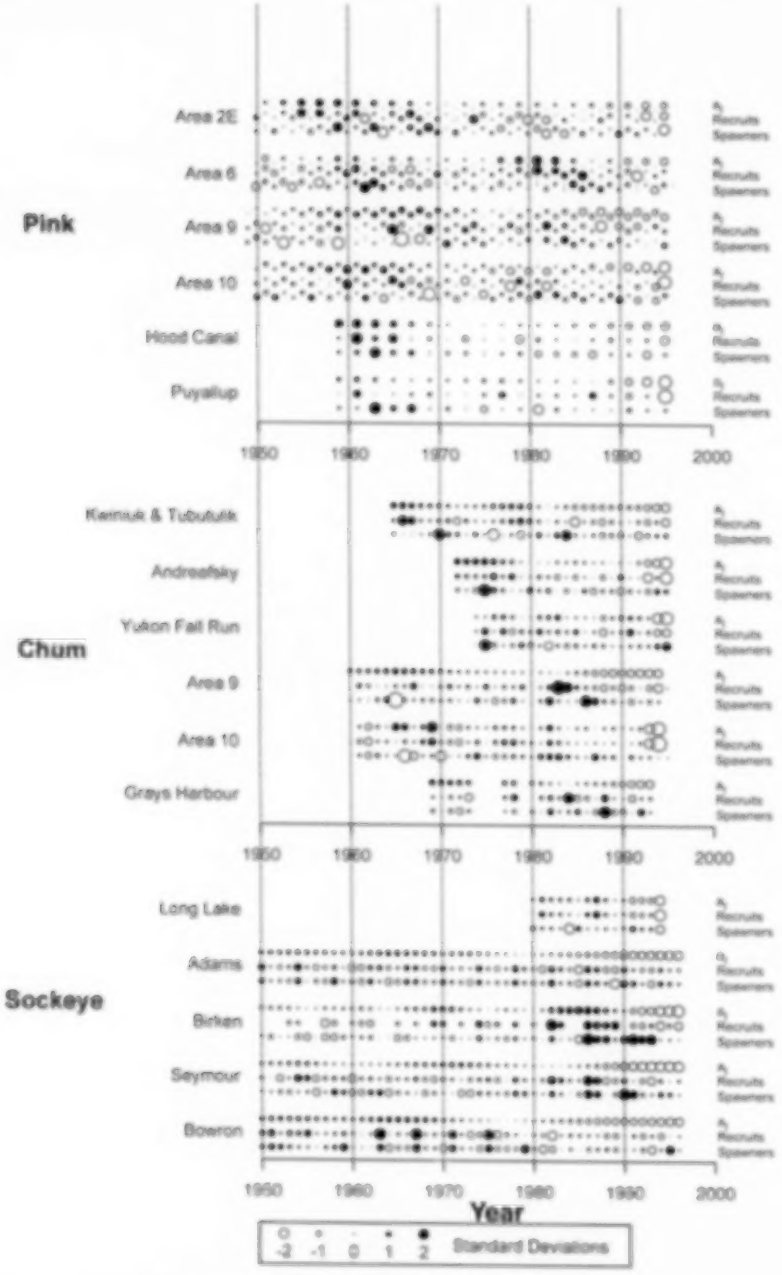
Fig. 8. Kalman-filtered a_y time series, recruitment, and spawner abundance for some stocks with low and (or) declining productivity in the 1990s. Like the Kalman-filtered a_y time series, spawner and recruit time series are scaled to a mean of zero and a standard deviation of one to highlight common patterns.



relevant to conservation and management, but different actions and concerns are affected (e.g., a given season's fishing plan or updates to a salmon stock's status, as opposed to long-term management or conservation planning).

The substantial temporal trends in productivity have important general implications for the conservation and management of salmon stocks. They suggest that the assumption of stationarity of parameters that is normally made in salmon stock–recruitment analyses may be inappropriate. If so, then using long data series to calculate management targets, such as escapement goals or target harvest rates, will reduce the chance of meeting management or conservation objectives, especially if those targets remain constant over many years, as they often do. For instance, if

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a sockeye salmon stock's a_t parameter decreases rapidly, then the standard Ricker model method for estimating target escapement (which depends in part on that a parameter) will put too much weight on older data (even when refit each year) and will not reflect the reduced mean productivity as promptly as a Kalman filter analysis, as demonstrated by Monte Carlo simulations comparing performances of the standard Ricker and Kalman filter methods (Peterman et al. 2000). The standard Ricker estimation method will thus be more likely to suggest an exploitation rate that is too high compared with a stock assessment method based on the Kalman filter that tracks such changes better. This difference in performance of the two methods results from their differing assumptions. The Ricker method (eq. 1) assumes that the productivity parameter was constant over the entire data set up through the latest data point. Thus, updating estimates annually with this model produces the average a value for the previous n years and repeats this process each year. In contrast, the Kalman filter method (eqs. 2, 3) is more flexible because it assumes that the productivity parameter a_t can differ each year of the data set, rather than being constant over some given period. An empirical analysis (Peterman et al. 2003) showed situations in which productivity of Bristol Bay, Alaska, sockeye salmon stocks decreased, but to meet management objectives, target escapements should have changed more than estimated by the standard Ricker analysis. That paper also showed analogous examples of the opposite situation, in which productivity increased, implying more improved prospects for sustainable harvest than a standard Ricker analysis.

Biologists have been well aware of such implications of temporal changes in salmon productivity for many years, but methods for dealing with them have been relatively ad hoc. For instance, Alaskan scientists have often split their sockeye salmon data sets into before and after 1976, the year that ocean productivity apparently increased dramatically and rapidly (H. Geiger, Alaska Department of Fish and Game, 1255 West 8th St., Juneau, Alaska, USA, personal communication). However, although that was an unusually large-magnitude event, it took about a decade for enough data to accumulate before that change became well-recognized by salmon scientists. Kalman filter analysis might have been able to highlight that change earlier and thus provide managers with more timely information on which to base their decisions.

To reduce the frequency of situations in which overexploitation leads to conservation concerns, salmon biologists may therefore want to consider using the Kalman filter version of the Ricker stock–recruitment model. The same can also be said for reducing the frequency of situations in which less harvest is taken than could be sustainable; fewer such situations will increase social and economic benefits from catching salmon. In both cases, the Kalman filter is a comparatively useful method for tracking changes in productivity relatively quickly (Peterman et al. 2000). The Kalman filter could also be beneficial in the context of future climatic change, about which there is large uncertainty concerning its effects on the direction and rate of change in productivity of Pacific salmon stocks in different locations (Beamish 1995).

However, analysis of Kalman-filtered a_t time series complements, rather than replaces, analysis of Ricker residuals. As noted above, at least some of the short-term variability apparent in the Ricker residuals, but not in the a_t time series, is highly correlated among stocks and likely reflects the influence of short-term variation in shared regional environmental forcing factors that is not well captured in the long-term signal estimated by the Kalman filter a_t time series. Because in this paper we are primarily interested in longer-term trends that are of special concern to management, our focus has been on smoothed Kalman filter a_t time series, but both indices reveal important aspects of temporal patterns in productivity. The juxtaposition of these indices in future research may help to differentiate between hypotheses about factors driving productivity within and across regions at different time scales.

Other methods for estimating temporal trends in salmon productivity could be compared with the Kalman filter in the future. For instance, some preseason forecasting models of salmon abundance use time-varying environmental covariates (e.g., Cass et al. 2006; Haeseker et al. 2008), and they could be applied retrospectively rather than just in a forecasting mode. If such mechanistically based models explain past variability well, then the nonmechanistic Kalman filter will be unnecessary for identifying shifts in underlying productivity. However, such mechanistically based models usually tend to not be very successful (Walters and Collie 1988; Myers 1998), so until reliable ones are found, a Kalman filter is probably the best option for describing past (not forecasting future) changes in underlying productivity. It works with spawner–recruit data and does not require environmental data. Furthermore, because a Kalman filter does not rely on covariates, it is not susceptible to climatic change altering parameters of existing relationships between environmental variables and productivity.

Mechanisms of change

There are at least three possible causes of the temporal changes in stock-specific a_t shown here. First, the population structure of a stock might have changed because of nonselective harvesting of co-migrating groups of fish, thereby causing less productive populations to gradually decrease in abundance and leaving mainly more productive populations. This could contribute to a gradual increase in a stock's productivity over time. Second, selective and heavy harvesting of the most productive populations composing a stock might have had the opposite effect, resulting in a gradual decrease in productivity of the aggregate stock. These two mechanisms related to harvesting pressure are unlikely, however, to explain the large and commonly observed reversal of time trends in productivity that we showed occurred during the study period. Thus, changing environmental conditions are another explanation that should be considered. For example, environmental changes may alter abundance and distribution of prey, predators, or competitors, or these changes may favor some age structure, life history types, or populations over others (Hilborn et al. 2003).

The importance of environmental factors in changing salmon productivity is supported by the correlations among our Kalman filter time series, which reveal positive covariation in productivity within and among certain regions that is consistent with shared environmental forcing factors at the re-

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gional scale. There was also a surprising number of high correlations between quite distant stocks, not necessarily because of sharing similar physical and biological conditions, but possibly because they had monotonic, smoothed a_i series, which would tend to lead to high correlations (either positive or negative). However, even if some of these high correlations between separate stocks were due to chance arising from similar but unrelated time trends, the large number of positive correlations suggests that at least some of these cases result from shared environmental effects at very large spatial scales.

Similar to Pyper et al. (2005), we found that changes in productivity for stocks within the same geographic region or within nearby regions tend to be positively correlated both within species and to some extent also between species. Although smoothing could create spurious correlations where none existed before, if real underlying patterns did not exist, we would not expect the correlations to be so systematic and similar across nearby regions. Compared with analyses of Ricker and Beverton–Holt residuals for most of the same stocks examined here (Peterman et al. 1998; Pyper et al. 2001, 2002), our analyses of Kalman-filtered a_i time series produced higher correlations and also more cases of high correlations between more distant regions. As mentioned above, the higher correlations may result because common environmental or biological drivers are more clearly expressed in the Kalman filter series than in the noisier Ricker and Beverton–Holt residuals, but the correlations could also be at least partially an artifact of the relative smoothness of the Kalman filter series. Time series were predominantly positively correlated for all three species among Alaskan stocks, whereas negative correlations predominated between Alaskan stocks and stocks from BC and Washington, especially for pink salmon and sockeye salmon (though not necessarily for chum salmon). These negative correlations are consistent with the findings of Hare et al. (1999) and Mueter et al. (2002), who found that indices of productivity for northern stocks have been dominated by historical trends that were opposite to those in southern stocks, suggesting that the stocks in these areas are subject to different environmental forcing factors or that they are affected in opposite ways by shared environmental conditions (Mueter et al. 2002).

The timing of major changes in productivity trends apparent in the a_i series also suggests a connection to atmospheric and (or) oceanographic forcing factors. We found that most stocks of the three species in Alaska experienced a period of very low productivity in the 1960s followed by a sharp increase throughout the 1970s, consistent with the major regime shift in physical conditions around 1976–1977 that has been well documented for the eastern North Pacific (e.g., Trenberth and Hurrell 1994; Mantua et al. 1997; Hare et al. 1999). Beamish et al. (1999) describes various indices of climatic drivers that also indicate major regime shifts in conditions during that same period and that are associated with substantial changes in aggregate salmon catches.

While our results are thus consistent with the hypothesis that in some cases longer-term changes in productivity are at least partially associated with corresponding changes in oceanographic conditions, we found some exceptions that indicate more complex responses to factors than previously thought. For example, major shifts in productivity trends, such as the one during the 1970s, did not always commence in the same year for all stocks affected, and both sockeye salmon and chum salmon stocks were often out of phase with their nearby conspecific stocks by several years. The explanation of these latter differences is unclear, but may be due to the interplay among environmental conditions and human-induced changes in habitats and amount of selective harvesting.

Differences among stocks

In addition to the productivity of stocks being slightly out of phase for some areas, large deviations from common regional patterns were also shown by individual component stocks, which again suggests complex responses to environmental drivers, human activities, or both. For instance, we identified several distinct "divergent" stocks that did not match the predominant regional pattern, including, among others, the Kodiak mainland and westside even-year pink salmon, Cook Inlet southern district even-year pink salmon, and sockeye salmon from Kodiak early and late Upper Station. Divergent stocks that do not conform to common regional productivity patterns might reflect real differences in biological or habitat conditions or might simply reflect factors such as relatively poor quality data on spawner abundance or an inappropriate level of aggregation of component populations (aggregation is expected to affect the quality of recruitment data through the extent of misallocation of catch to spawning stocks). However, poor data quality and aggregation appear unlikely as an explanation for most divergent stocks. For instance, Fraser River sockeye spawner and recruit data are considered some of the highest-quality data available, yet we showed above that the 16 stocks diverge considerably in their temporal patterns in a_i. Such differences among stocks also occur, but to a lesser extent, for Bristol Bay sockeye data, which are again considered high quality. In contrast, southeast Alaska pink spawner abundance data are viewed as much more uncertain, yet we showed a strong positive correlation among those a_i series. We believe that our results represent a conservative, one-sided interpretation of actual within-region coherence of productivity patterns. That is, cases in which we found an apparently highly correlated group of stocks may in fact include some stocks that are divergent, but the reverse is less likely to be true (i.e., a group of apparently uncorrelated or weakly correlated stocks is unlikely to be highly correlated in reality).

To the extent that the divergent series of Kalman filter a_i represent real diversity in life history traits or environmental conditions within a region, these a_i series and cases of low or negative correlations between these data series help identify components important for monitoring or conservation. For example, certain stocks within an area might be particularly sensitive (or insensitive) to climate-driven disturbances such as low water levels, flooding, or high water temperatures because of their run timing or the nature of their habitat. Consequently, large-scale climatic shifts may affect some stocks differently than others and may represent potential compensatory responses to environmental changes. Thus, special attention should be paid to monitoring stocks that deviate from the dominant productivity patterns in the

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area. Conversely, groups of stocks with highly synchronous productivity trends, such as the Chignik and Alaska Peninsula pink salmon, may have limited ability to buffer the effects of environmental changes, at least with respect to the drivers that have historically been most important. It is especially important in such groups of stocks to recognize declining trends in productivity early and implement precautionary measures to reduce potential ecological and socio-economical impacts of low recruitment.

Though the extent of aggregation represented by our Pacific salmon stocks is too large to provide advice on efficient designs of monitoring programs, our data provide some pertinent information. In particular, our results underscore the importance of maintaining extensive, high-quality monitoring programs for spawners and catches by stock because of the large changes in productivity documented here. This is particularly important given the potential for future climatic and human-induced changes in marine and freshwater habitats. Without such monitoring programs, it might be difficult to detect and respond to reductions in productivity in an appropriate and timely manner. That monitoring, combined with the Kalman filter estimation procedure, can help to identify conservation and management issues related to productivity.

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Potential limits to anthropogenic mortality of small cetaceans in coastal waters of British Columbia

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Abstract: Small cetaceans are by-caught in salmon gillnet fisheries in British Columbia (BC) waters. In Canada, there is currently no generic calculation to identify when management action is necessary to reduce cetacean bycatch below sustainable limits. We estimated potential anthropogenic mortality limits for harbour (*Phocoena phocoena*) and Dall's (*Phocoenoides dalli*) porpoises and Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) using quantitative objectives from two well-established frameworks for conservation and management (the United States' Marine Mammal Protection Act and the Agreement on the Conservation of Small Cetaceans of the Baltic and North Seas), which are similar to some management objectives developed for marine mammal stocks elsewhere in Canada. Limits were calculated as functions of (*i*) a minimum abundance estimate (2004–2005); (*ii*) maximum rate of population increase; and (*iii*) uncertainty factors to account for bias in abundance estimates and uncertainty in mortality estimates. Best estimates of bycatch mortality in 2004 and 2005 exceeded only the most precautionary limits and only for porpoise species. Future research priority should be given to determining small cetacean stock structure in BC and refining species-specific entanglement rates in these and other fisheries. The approach offers a quantitative framework for Canada to meet its stated objectives to maintain favourable conservation status of cetacean populations.

Résumé : Des petits cétacés se retrouvent parmi les captures accessoires des pêches au saumons au filet maillant dans les eaux de la Colombie-Britannique (BC). Au Canada, il n'y a pas de calcul générique pour déterminer quand des actions de gestion sont nécessaires pour réduire les prises accessoires de cétacés sous un seuil durable. Nous estimons les limites potentielles de la mortalité due aux facteurs anthropiques chez le marsouin commun (*Phocoena phocoena*), le marsouin de Dall (*Phocoenoides dalli*) et le lagénorhynque à flancs blancs du Pacifique (*Lagenorhynchus obliquidens*) à l'aide d'objectifs quantitatifs provenant de deux cadres de référence bien établis pour la conservation et la gestion (la loi américaine sur la protection des mammifères marins et l'accord sur la conservation des petits cétacés dans la Baltique et la mer du Nord), qui possèdent certains des objectifs mis en place pour les stocks de mammifères marins ailleurs au Canada. Les limites ont été calculées en fonction (*i*) d'une estimation d'abondance minimale (2004–2005), (*ii*) du taux maximal d'accroissement de la population et (*iii*) de facteurs d'incertitude qui tiennent compte de l'erreur dans les estimations d'abondance et de l'incertitude dans les estimations de mortalité. Les meilleures estimations de la mortalité due aux captures accessoires en 2004 et 2005 ne dépassent que les limites les plus prudentes et seulement dans le cas des espèces de marsouins. Les priorités futures de recherche devraient inclure la détermination de la structure du stock des petits cétacés en BC et la précision des taux d'empêtrement en fonction des espèces dans ces pêches et dans les autres. Notre approche fournit un cadre quantitatif pour que le Canada atteigne ses objectifs avoués de maintenir un état de conservation favorable pour les populations de cétacés.

[Traduit par la Rédaction]

Introduction

The effects of fishery-related mortality on small cetacean populations around the world have long been known to be an important conservation factor (Read et al. 2006). For some, such as vaquita (*Phocoena sinus*), it may be the driving factor in population decline (D'agrosa et al. 2000). In 1991, the International Union for the Conservation of Nature stated that the single most important action needed to protect the harbour porpoise (*Phocoena phocoena*) was to reduce incidental take in gill nets and other fishing gear (Klinowska 1991).

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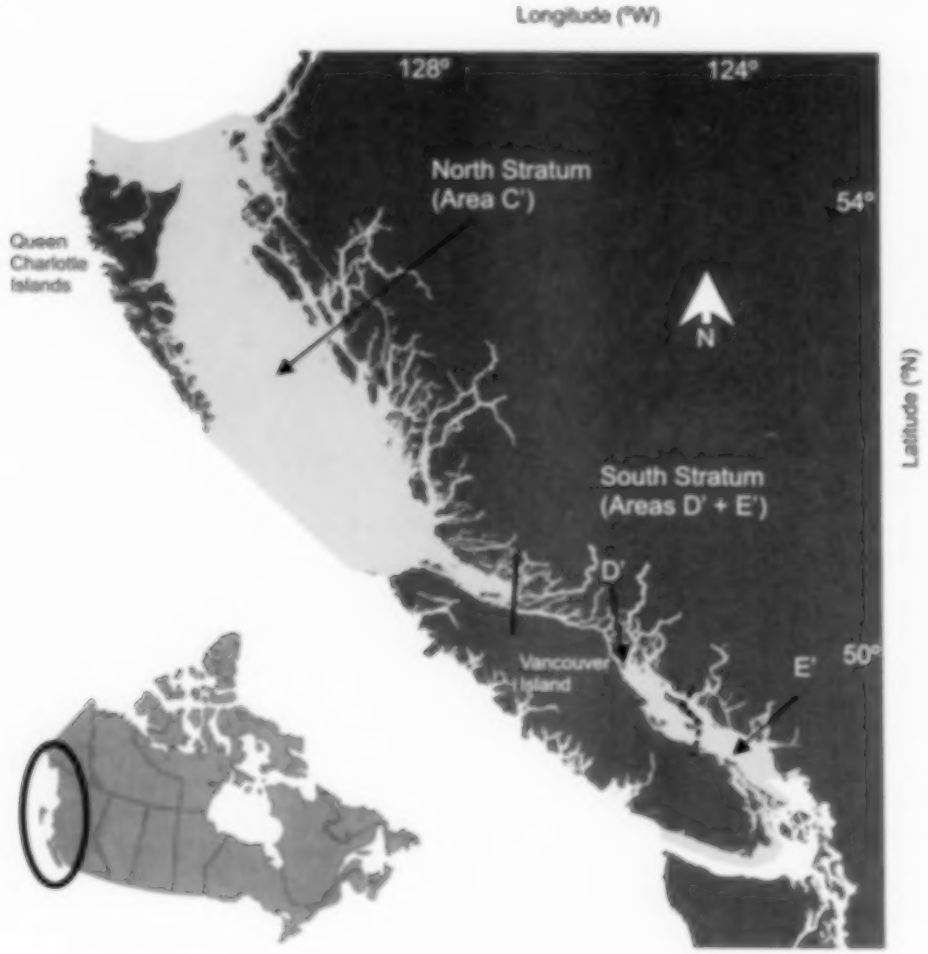
Fig. 1. Study area delineated by black oval on map of Canada (inset). The North stratum is equivalent to our area C′ (i.e., the inshore section of Fisheries and Oceans Canada's (DFO) Salmon Licensing Area C), which is composed of DFO Salmon Gillnet Management Areas 1–11 plus one-half of Area 12. The South stratum contains our areas D′ and E′ (i.e., the inshore section of DFO's Salmon Licensing Areas D and E), which are composed of the DFO Salmon Gillnet Management Areas 13–15 plus one-half of Area 12 (D′) and Areas16–20 plus Areas 28–29 (E′).



Bycatch mitigation measures are not typically driven by animal welfare needs, but rather by some balance between conservation consequences to populations and economic costs to fisheries. In eastern Canada, much effort has been directed successfully at reducing the incidental mortality of Atlantic harbour porpoise (Read and Gaskin 1988; Brodie 1995; Caswell et al. 1998). These and many other coordinated efforts evaluated estimated population sizes, stock boundaries, rates of growth, and rates of fishery-related mortality (removals) to determine whether the rate of removal was greater than the intrinsic rate of population growth (Lawson et al. 2004; Lesage et al. 2006). If so, management actions were triggered that involved the scientific, management, conservation, and fishing communities to reduce anthropogenic mortality of porpoise in Atlantic Canadian waters (Woodley 1995; Trippel et al. 1996).

On the Pacific coast of the USA and Canada, many cetacean species, including harbour porpoise, Dall's porpoise (*Phocoenoides dalli*), and Pacific white-sided dolphins (*Lagenorhynchus obliquidens*), are killed in coastal fisheries (Barlow et al. 1994; Gearin et al. 1994; Stacey et al. 1997). Mortality levels vary by location, fishery, species, season, and year; however, the harbour porpoise appears to be one of the most frequent victims of incidental mortality in commercial gear in British Columbia (BC) and Washington (Gearin et al. 1994; Baird and Guenther 1995; Stacey et al. 1997).

In Canada's Pacific region (Fig. 1), harbour porpoise are considered a species of "Special Concern" because the species is considered to be highly sensitive to human activities, is prone to becoming trapped or killed in fishing nets, and is being seen more rarely in highly developed areas, such as

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the waters near Victoria and Haro Strait (COSEWIC 2003). In Washington, the Inland Waters Stock (delineated as east of the northward line from Cape Flattery, Washington) is not listed as "strategic" because the species is not listed as "depleted" under the US Marine Mammal Protection Act (MMPA) or as "threatened" or "endangered" under the Endangered Species Act (NMFS 2006). However, based on the best estimates of bycatch relative to fishing effort in Washington, the National Marine Fisheries Service of the United States maintains that the total fishery mortality and serious injury for the Washington Inland Waters Stock cannot be considered to be insignificant (NMFS 2006). Understanding the population-level effects of bycatch in the inland waters is complicated by a lack of knowledge of transboundary movements of harbour porpoise and the extent to which these porpoises are subject to fishery-related mortality in BC (Hall et al. 2002; NMFS 2003; NMFS 2006).

In contrast, Dall's porpoise and Pacific white-sided dolphins are designated as "Not at Risk" by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC), because there are not thought to be any major threats to their long-term survival (Baird and Stacey 1989; Jefferson 1989). However, it should be noted that the status of these species has not been assessed since 1989 and 1990, respectively.

Dall's porpoise are known to frequent the transboundary waters of BC and Washington, whereas Pacific white-sided dolphins are only occasional visitors (Calambokidis and Baird 1994). With regard to the latter, there have been an increased number of sightings in inland BC waters since their COSEWIC listing (Morton 2000). It is also well known that fisheries technology and fishing gear have changed in that time. As with harbour porpoise, the amount of transboundary movement remains unknown.

The most recent study on small cetacean bycatch in BC (Hall et al. 2002) indicates that all three species have been caught and killed in coastal net fisheries during the time that has elapsed since the COSEWIC designations. Using direct and indirect data collection techniques, Hall et al. (2002) determined probabilities of entanglement and mortality yielding up to an estimated 100 small cetaceans killed in the commercial salmon gillnet fisheries in 2001. It was expected that different numbers of harbour porpoise, Dall's porpoise, and Pacific white-sided dolphins would be killed annually owing to changing ecological conditions and the variable nature of the fisheries (Hall et al. 2002). Previously, it has been impossible to put these estimates of bycatch in a conservation or management context, because of lack of (*i*) estimates of small cetacean abundance in BC coastal waters and (*ii*) quantitative management objectives and threshold mortality limits.

Summertime estimates of abundance have since become available for several marine mammal species in BC coastal waters. A design-unbiased survey was planned (Thomas et al. 2007) and conducted (Williams and Thomas 2007) in 2004 and 2005 and included BC inshore coastal waters (with a north–south extent from the BC–Alaska to the BC–Washington borders and an east–west extent from the mainland of BC to a line joining the north end of Vancouver Island to the south end of the Queen Charlotte Islands). Using small-boat surveys, Williams and Thomas (2007) estimated the average summertime (2004–2005) abundance of harbour porpoise in the study area to be 9120 animals (95% confidence interval, CI: 4210–19 760). Abundance estimates were also presented for Dall's porpoise (4910 animals, 95% CI: 2700–8940) and Pacific white-sided dolphins (25 900 animals, 95% CI: 12 900–52 100). These estimates are preliminary and made two key assumptions: all animals on the trackline were detected (the so-called "g(0)=1" assumption), and animal positions were recorded prior to movement in response to the boat (the assumption of no responsive movement).

Small cetacean conservation requires understanding the consequence of fisheries bycatch at the population level and having a management framework in place that motivates action when predetermined thresholds are exceeded. Though the studies of Williams and Thomas (2007) and Hall et al. (2002) were designed with independent objectives, together, the two provide data that may facilitate an attempt at calculating bycatch mortality threshold levels for small cetaceans that would trigger mitigation measures aimed at gear entanglement reduction.

The estimation of a threshold bycatch mortality limit requires two things: (*i*) management–conservation objectives and (*ii*) a procedure for calculating the maximum level of mortality that will still achieve those objectives (Johnston et al. 2000). Management objectives for conservation have recently been articulated in quantitative terms for some marine mammal stocks in Canada (e.g., Hammill and Stenson 2007), but there is currently no generic set of national objectives for all stocks. Similarly, threshold mortality limits (allowable harm) have been calculated for marine mammal stocks as part of Recovery Potential Assessments under the Canadian Species at Risk Act, but there is currently no uniform approach to calculating mortality limits.

In the USA, cetaceans are protected under the MMPA, which triggers conservation and management action when bycatch exceeds a specific mortality limit known as potential biological removal (PBR) (Wade 1998). The calculation of the PBR limit is straightforward given an estimate of population size, and the method was designed to achieve a management objective of maintaining marine mammal populations at or above their maximum net productivity level (as legislated in the MMPA). The PBR technique was designed to be conservative; for example, as uncertainty in abundance estimates increase, the PBR limits decrease (Wade 1998). While PBR is formally entrenched in US law, the PBR approach has also been used more generally to provide guidance when assessing the sustainability of bycatch of small cetaceans in many other countries (e.g., Berggren et al. 2002; Slooten et al. 2006).

Here, we report on a preliminary attempt to calculate threshold limits to anthropogenic mortality for small cetaceans in BC coastal waters. In the absence of defined Canadian management objectives and mortality limits to protect small cetacean populations from incidental mortality in fisheries, we used the PBR approach to calculate mortality limits based on the conservation objectives of two well-established, international frameworks for conservation and management: the US MMPA; and the Agreement on the Conservation of Small Cetaceans of the Baltic and North Seas (ASCOBANS). These objectives are similar in nature to management objectives outlined for other marine mam-

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mal stocks in Canada (Hammill and Stenson 2007). We then compare the estimated mortality limits with current estimates of small cetacean bycatch to determine whether the current mortality levels are consistent with the conservation objectives set by either the MMPA or ASCOBANS. We make no value judgement as to what Canada's quantitative management objectives ought to be. Instead, we apply a commonly used procedure with two sets of quantitative objectives to assess how the BC salmon gillnet fishery measures up in light of Canada's stated management objectives to maintain favourable conservation status of cetaceans in its territorial waters.

Materials and methods

Geographic areas

We restricted our analyses to the study area of Williams and Thomas (2007), that is, inshore BC waters for which small cetacean abundance estimates exist (Fig. 1). All waters on the west coasts of Vancouver Island and the Queen Charlotte Islands were excluded. These coastal waters were subdivided on the basis of Canadian Commercial Gillnet Fishing Areas – Pacific Region for salmon (www-ops2.pac.dfo-mpo.gc.ca/ops/vrndirectory/AreaDsc.cfm). Estimation of bycatch, as related to the study area of Williams and Thomas (2007), required grouping the salmon fishery statistical licensing areas. We adjusted the boundaries of the federally recognized fishing areas known as Salmon Licensing Areas C, D, and E so that they corresponded roughly to the northern and southern strata of Williams and Thomas (2007, Fig. 1). We refer subsequently to these salmon areas as C′, D′, and E′, such that C′ = Salmon Gill Net (SGN) Areas 1–11 plus one-half of Area 12; D′ = SGN Areas 13–15 plus one-half of Area 12; and E′ = SGN Areas 16–20 plus Areas 28–29. Area C′ corresponds generally to the Queen Charlotte Basin and adjacent mainland inlets and is referred to subsequently as our North stratum. Areas D′ and E′ refer to south coast waters (Johnstone Strait, Strait of Georgia, and Strait of Juan de Fuca) plus their connecting channels and adjacent inlets. These are subsequently referred to as our South stratum.

Population structure

The population structures of small cetaceans within BC waters are currently not known. Genetic and contaminant loading evidence indicates that eastern North Pacific harbour porpoise are not panmictic (i.e., there is evidence to suggest that there is stock structure within the region) and low levels of genetic mixing occur along the west coast of North America (Calambokidis and Barlow 1991; Chivers et al. 2002; NMFS 2006). Stock boundaries may exist within BC and Washington waters; however, the number, range, relative sizes, and rate of mixing requires further investigation. Given the evidence for fine-scale stock structure in harbour porpoise, it seemed appropriate to consider three scenarios for harbour porpoise: (*i*) a single BC stock (Areas C′ + D′ + E′); (*ii*) two stocks split on a north (Area C′) – south (Areas D′ + E′) basis based on coastal geography; and (*iii*) a transboundary scenario in which the southern BC and the Washington State Inland Waters stocks formed a single stock. Stock structures of Dall's porpoise and Pacific white-sided dolphins are similarly unstudied in BC; however, there is little evidence from adjacent waters to suspect as much fine-scale stock structure in these species as is found in harbour porpoise. Therefore, we consider only the scenario of a single stock for Dall's porpoise and Pacific white-sided dolphins.

Abundance estimates

Data on small cetacean density and abundance came from a design-unbiased, systematic survey (Thomas et al. 2007) for which field methods, data analyses, and preliminary results have been previously described (Williams and Thomas 2007). We used the published information on stratum area and animal density to estimate animal abundance for northern (C′) and southern (D′ + E′) waters. This process assumed that animal density was uniform within the four survey strata of the Williams and Thomas (2007) study.

To make our abundance estimates correspond spatially to the SGN areas, we had to add the estimated number of small cetaceans in mainland inlets to their counterparts in adjacent Inside Passage waters. For the 32 mainland inlets in the fjord stratum of Thomas et al. (2007), 68.1% of the area was estimated to fall in northern (C′) waters and 31.9% in southern (D′ + E′) waters. To obtain coefficients of variation (CVs) for the combined North and South strata, we first calculated CVs for the northern and southern parts of the fjord stratum (Williams and Thomas 2007). We did this assuming that the overall variance of the fjord stratum was equal to the sum of the variances of the northern and southern parts of the fjord stratum (assumed to be independent) and assuming that the CVs of the northern and southern parts were equal (Seber 1982):

$$V_{fjord} = \left(N_{nfjord}\mathrm{CV}_{nfjord}\right)^2 + \left(N_{sfjord}\mathrm{CV}_{sfjord}\right)^2$$

where V_{fjord} is the total variance; assuming that $\mathrm{CV}_{nfjord} = \mathrm{CV}_{sfjord}$, rearranging to solve for this CV gives

$$\mathrm{CV}_{nfjord} = \mathrm{CV}_{sfjord} = \sqrt{\frac{V_{fjord}}{N_{nfjord}^2 + N_{sfjord}^2}}$$

These CVs for the northern and southern parts of the fjord stratum were then converted to variances and added to the variances of the other estimates corresponding to our North and South strata to get overall variances (and CVs) for these combined abundance estimates.

Two outstanding issues with existing estimates of abundance are responsive movement and diving animals missed on the trackline. Responsive movement can introduce positive or negative bias in abundance estimates, depending on whether the animal moved to approach or avoid the vessel, respectively. Responsive movement was assessed by examining the behaviour data recorded at the time of the first sighting. If animals were attracted to the ship, then the proportion of sightings scored as being oriented toward the vessel would be higher than one would predict from chance alone, and vice versa. The standard methods used for assessing responsive movement issues from behavioural data are described by Palka and Hammond (2001).

The problem of missing animals on the trackline ($g(0) < 1$) is difficult to assess from a small boat. Many methods have been developed to estimate $g(0)$ using double plat-

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form experiments on large ships, but isolating independent observer platforms on a small vessel is problematic. Until we can address this issue in the field, we conducted a literature review to identify estimates of g(0) that other researchers have calculated for harbour porpoise on shipboard surveys.

Calculation of mortality limits using default methods for PBR and tuning simulations

PBR

Under the PBR procedure, the limit to removals (i.e., anthropogenic mortality) for a management area is calculated using a relatively simple equation and a current estimate of absolute abundance (Wade 1998):

$$\text{(1)} \qquad \text{PBR} = N_{\min}\frac{1}{2}R_{\max}F$$

where PBR is the potential biological removal limit, $N_{\min}$ is the minimum estimated number of animals, $R_{\max}$ is maximum population growth rate (i.e., at low density), and F is a recovery factor — a parameter that can be tuned so that the PBR procedure achieves specific management objectives. We assumed an $R_{\max}$ of 0.04 following Wade (1998) and because 4% is a plausible lower value for the maximum rate of increase of a harbour porpoise population (Barlow and Boveng 1991; Woodley and Read 1991; International Whaling Commission 2000). Errors in estimates of abundance from surveys are assumed to be lognormally distributed, so that $N_{\min}$ is calculated as

$$\text{(2)} \qquad N_{\min} = O_{\text{abs}}\exp\left[Z\sqrt{\log\left(1+\text{CV}_{\text{abs}}^2\right)}\right]$$

where O_{abs} is a survey estimate of absolute abundance, CV_{abs} is the coefficient of variation of this estimate, and Z is a standard normal deviate corresponding to a specified percentile (fixed at –0.842 for the 20th percentile following Wade 1998). Equation 2 assumes that O_{abs} is the median of the error distribution around O_{abs}.

Simulation model

A simulation model was used to tune the PBR procedure to specific management objectives. The model simulated a "known" small cetacean population over time, while simulating observation of this population and the implementation of the PBR procedure. Importantly, the procedure did not have knowledge of the known population; it only operated on the simulated observed data.

The model of the known population was a simple logistic model:

$$\text{(3)} \qquad N_{t+1} = N_t\left[1+R_{\max}\left(1-\frac{N_t}{K}\right)\right]-C_t$$

where $R_{\max}$ is maximum population growth rate (assumed to be 0.04), K is population size at carrying capacity, and C_t is realized removals in year t. Realized removals were modelled as a random deviation from the set PBR limit for year t (PBR_t):

$$\text{(4)} \qquad C_t = N\left[\text{PBR}_t, (\text{PBR}_t\text{CV}_{\text{byc}})^2\right]$$

where CV_{byc} is the coefficient of random variation in removals (assumed to be 0.5 based on our assumed CV in the rate of entanglement; see below) and $N(\mu,\sigma^2)$ is a random normal variable with expectation μ and variance σ^2. Random deviations from the PBR limit were assumed to be independent between years.

Survey estimates of absolute abundance (O_{abs_t}) were simulated every 10 years for input to the PBR procedure. Errors in these estimates were assumed to be independent between years and surveys and lognormally distributed so that

$$\text{(5)} \qquad O_{\text{abs}_t} = \exp\left\{N\left[\log\left(\frac{N_t}{\sqrt{1+\text{CV}_{\text{abs}_t}^2}}\right), \log\left(1+\text{CV}_{\text{abs}_t}^2\right)\right]\right\}$$

PBR was calculated immediately after a survey for absolute abundance (eqs. 1 and 2), and this annual bycatch limit was used until the next survey.

Simulations were initialized by setting the initial number of animals in the population to a proportion of the number of animals at carrying capacity (D_0). In each individual simulation, D_0 was randomly drawn from a uniform distribution ranging from 0.05 to 1.

Tuning simulations

The PBR procedure was tuned (i.e., determined appropriate value for F) so that long-term population status achieved a given conservation objective with 95% probability. Two conservation objectives were considered.

The first was the objective used in the original development of the PBR procedure (Wade 1998): recover and (or) maintain the population at or above 50% of carrying capacity (the likely lower limit for maximum net productivity level). The second objective was that of ASCOBANS: recover and (or) maintain the population at or above 80% of carrying capacity. Survey CVs used in the tuning simulations corresponded to the actual survey CVs, which were also used in the PBR calculations described below. We ran 1000 simulations for each tuning.

PBR limit calculations

PBR limits were calculated using eqs. 1 and 2 and survey estimates of abundance for two different tunings (two objectives) and for the three population structure scenarios: (*i*) entire survey area; (*ii*) north–south strata; and (*iii*) transboundary scenario. PBR limits were also calculated allowing abundance estimates to be underestimates owing to animals being missed on the trackline. Abundance estimates were

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Table 1. Harbour porpoise (*Phocoena phocoena*) abundance estimates and coefficients of variation (CV).

	N	CV	Variance
Williams and Thomas (2007) strata			
1 (Queen Charlotte Basin)	4587	0.52	5667509
2 (Johnstone Strait and Discovery Passage)	0	0	0
3 (Strait of Georgia and Juan de Fuca Strait)	3391	0.46	2422596
4 (Mainland inlets)	1140	2.26	6637837
4a (Mainland inlets corresponding to stratum 1)	776	3.01	5443130
4b (Mainland inlets corresponding to strata 2–3)	364	3.01	1194707
Williams and Thomas (2007) whole area	9118	0.420892741	14727941
New area			
North (stratum 1 plus corresponding inlets)	5363	0.621494202	11110639
South (strata 2–3 plus corresponding inlets)	3755	0.506544583	3617303
Transboundary area			
Southern BC plus Washington inland waters	14437	0.633236	334292278

divided by 0.5 and 0.8 for harbour and Dall's porpoise, respectively, which are reasonable estimates of g(0) for these species (Barlow et al. 1997). PBR limits were then recalculated with the adjusted abundance estimates. No bias was expected in estimates of Pacific white-sided dolphin abundance because of high detectability expected for these acrobatic and gregarious animals (Williams and Thomas 2007; Barlow et al. 1997). Responsive movement was addressed for Pacific white-sided dolphins in previous analyses (Williams and Thomas 2007).

Estimating bycatch entanglement and bycatch mortality

Probabilities of entanglement (P_{ent}) and mortality rates in BC were reported by Hall et al. (2002) for the commercial salmon gillnet fleet based on observer and license holder data. P_{ent} and mortality rates were regionally determined with two independent data sets: (*i*) observer data from southern BC and (*ii*) province-wide commercial license holder data (Hall et al. 2002).

We used the south coast probability of entanglement on a per-boat-day-fished (BDF) basis and mortality rate as reported by Hall et al. (2002) (n = four small cetaceans entangled in 3236 BDF with 5% observer coverage: P_{ent} = 0.0247 animal-BDF^{-1}, mortality rate of observed entangled animals = 50%). The fishing effort in BDF reported for each area in 2004 and 2005 was simply multiplied by this probability and mortality rate to yield estimates of bycatch mortality for our northern and southern strata.

Hall et al. (2002) cautioned that such extrapolations must be exercised with vigilance because of the uncertainties associated with small sample sizes and the assumptions that the 5% observer coverage was representative of the entire salmon fleet and that P_{ent} was spatially and temporally equal. For example, it is likely that the number of animals entangled per unit fishing effort is a function of animal density. Unfortunately, there are no estimates of density available for the years of the entanglement rate data with which to adjust entanglement rates by animal density. It is also important to note that these rate estimates were based on a sample size of four animals, of which two were confirmed as harbour porpoise, one Dall's porpoise, and one small cetacean for which species identification was not available. However, in the absence of finer-scale data, they remain the only available data from which to work to obtain point estimates of mortality rate.

To illustrate uncertainty surrounding the mortality estimates, we calculated two additional rates of entanglement using the upper and lower 95% confidence limits as also presented by Hall et al. (2002). In 2001, observer coverage was 5%, and total fishing effort was 3236 BDF. This corresponds to 161.8 BDF monitored, with four animals reported entangled. Setting this as a single observation in a Poisson distribution yields 95% confidence limits of 1.09–10.24 animals entangled·162 BDF^{-1}, with a CV of 0.5 (Hall et al. 2002; Zar 1996). Using these bounds as the theoretical minimum and maximum number of animals caught within the observed number of days (161.8 BDF) allows estimation through linear extrapolation to the likely range within which the actual levels of mortality fall. The lower limit was estimated using P_{ent} = 0.0067 (1.09 animals·161.8 BDF^{-1}), while the upper limit was estimated using P_{ent} = 0.0633 (10.24 animals·161.8 BDF^{-1}).

It is likely that our confidence interval based on the Poisson distribution underestimates the uncertainty in the number of animals entangled per unit of observed fishing effort. The quasi-Poisson or negative binomial distributions, which allow for overdispersion relative to the Poisson distribution, might be more appropriate. However, with so few observed events it was not possible to reliably estimate how overdispersed these data might be. Our confidence interval for the rate of entanglement should be considered a minimum confidence interval.

Results

Area-specific estimates of harbour porpoise abundance are provided (Table 1). A number of estimates of g(0) have been reported for harbour porpoise from shipboard sightings surveys. Barlow et al. (1997) reviewed g(0) estimates reported from shipboard surveys for harbour porpoise in US waters that ranged from 0.4 to 0.78, depending, inter alia, on number of observers and sighting conditions (with three observers and good sighting conditions producing the highest detection probability). Palka (2000) conducted shipboard sightings surveys for harbour porpoise in the Gulf of Maine

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Table 2. Proposed limits to anthropogenic mortality (ML) for small cetaceans in inshore waters of BC, using two different management objectives and incorporating likely scenarios for bias in abundance estimates.

				ML		
Area	*N* (CV)	Objective	*F*	g(0) = 1	g(0) = 0.5	g(0) = 0.8
Harbour porpoise						
Entire coast	9 118 (0.42)	0.5	1	129	259	
		0.8	0.41	53	106	
North	5 363 (0.62)	0.5	1	66	132	
		0.8	0.43	28	57	
South	3 755 (0.51)	0.5	1	50	100	
		0.8	0.42	21	42	
BC (South)–WA	14 437 (0.31)	0.5	1	223	447	
		0.8	0.40	89	178	
Dall's porpoise						
Entire coast	4 913 (0.29)	0.5	1	77		96
		0.8	0.40	30		38
Pacific white-sided dolphin						
Entire coast	25 906 (0.35)	0.5	1	388		
		0.8	0.41	159		

Note: The objective labelled 0.5 corresponds to a conservation objective of maintaining populations at or above 50% of *K* with 95% confidence, which equates roughly to the default values of the potential biological removal (PBR) calculations under the US Marine Mammal Protection Act (MMPA). The objective labelled 0.8 corresponds to a conservation objective of maintaining populations at 80% of *K* with 95% confidence, which equates to the management objectives under the Agreement on the Conservation of Small Cetaceans of the Baltic and North Seas (ASCOBANS).

and Bay of Fundy that produced estimates of g(0) ranging from 0.25 to 0.74, depending on platform height (9 or 14 m above the sea surface), number of observers, and stratum. Clearly, our estimate of harbour porpoise abundance is negatively biased to some degree. Williams and Thomas (2007) note that their small-boat surveys, by necessity, were conducted in good sighting conditions and always with a team of three observers. We suspect that g(0) for the Williams and Thomas (2007) survey for harbour porpoise was high (~0.75). For illustrative purposes, we calculate PBR across a range of plausible values by calculating what PBR would be if g(0) were 1 or 0.5.

Applying the methods of Palka and Hammond (2001) to our behavioural data, we found no evidence that responsive movement (avoidance or attraction) was a problem for harbour or Dall's porpoises. (Previous analyses (Williams and Thomas 2007) addressed attractive movement by dolphins.) Failure to detect significant effects suggests that any bias due to unmodelled responsive movement was negligible. Harbour porpoise are known to avoid ships (Palka and Hammond 2001), so avoidance behaviour would serve to underestimate abundance. We have no evidence to support including this as a bias parameter, and any unmodelled bias would only increase PBR. We conclude that this is a small problem at most and one that can be ignored in a precautionary framework.

Estimated mortality limits

Mortality limits were relatively low because of the large CVs associated with the estimates of abundance and bycatch (Table 2). Our abundance estimates were relatively imprecise, as expected for a small-boat survey.

Table 3. Estimates of total mortality of small cetaceans from the 2001 fisheries observer coverage and 2004 and 2005 gillnet fishing effort in boat-days fished (BDF).

Salmon area	BDF	Estimated no. entangled (BDF × P_{ent})	Estimated mortality
2004			
C	12 480	308.14	154.07
D	1 610	39.75	19.88
E	1 620	40	20.00
Total			194
2005			
C	8 605	212.73	106.37
D	1 225	30.28	15.14
E	730	18.05	9.02
Total			131

Estimates of total bycatch in 2004 and 2005 fisheries

Observer data

Estimates of small cetacean bycatch in the 2004 and 2005 BC salmon gillnet fishery were based on the annual BDF within the survey area of Williams and Thomas (2007) and on P_{ent} and mortality rate estimated by Hall et al. (2002). Estimates of total small cetacean mortality were determined using the observer-derived P_{ent} = 0.0247 and mortality rate = 50% of Hall et al. (2002). Point estimates of bycatch (entanglement) and mortality are provided (Table 3).

To aid in presenting the uncertainty associated with these mortality point estimates, a Poisson distribution was used to

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Table 4. Confidence intervals for estimates of total mortality of small cetaceans in 2004 and 2005.

Year	Total BDF	Lower P_{ent}	Lower 95% CL	Upper P_{ent}	Upper 95% CL
2004	15 710	0.0067	52.85	0.0632	497
2005	10 560	0.0067	35.53	0.0632	334

Note: BDF, boat-days fished; P_{ent}, probability of entanglement; CL, confidence limit.

Table 5. Estimates of small cetacean gillnet-fisheries-related mortality based on entire coast point estimates of total mortality (Table 3) and three scenarios incorporating uncertainty in species identification from Hall et al. 2002.

		Mortality	
Species	Percentage	2004	2005
Scenario 1			
Harbour porpoise	50	97	66
Dall's porpoise	25	49	33
Pacific white-sided dolphin	25	49	33
Scenario 2			
Harbour porpoise	50	97	66
Dall's porpoise	50	97	66
Pacific white-sided dolphin	0	0	0
Scenario 3			
Harbour porpoise	75	146	98
Dall's porpoise	25	49	33
Pacific white-sided dolphin	0	0	0

ascertain upper and lower confidence limits (shown in Table 4).

Hall et al. (2002) indicated that bycatch in the salmon gillnet fishery most often consisted of harbour porpoise, with Dall's porpoise and Pacific white-sided dolphins being caught less often. To get species-specific estimates of mortality, three scenarios were explored based on species proportions reported in Hall et al. (2002) and our point estimates (Table 5).

License holder data

An independent estimate of P_{ent} for harbour porpoise was obtained in 2001 using a province-wide questionnaire to license holders (Hall et al. 2002). From this, Hall et al. (2002) estimated a mortality rate of 47% and P_{ent} = 0.0152 per license holder per year. Lower estimates of P_{ent} and mortality resulted from this coast-wide evaluation (Table 6). This lower rate may be due to a real effect, that is, a lower entanglement rate in north coast waters than in south coast waters, or to an apparent effect, that is, lower rates of bycatch relating to self-reporting compared with independent observer-obtained data. However, supplementary data collected by Hall et al. (2002) that spanned more than 20 years supported the initial results, indicating that bycatch of small cetaceans in the BC salmon gillnet fishery is a rare event.

The estimates in Table 6 only include harbour porpoise. Recall that harbour porpoise were found to compose either 50% or 75% of by-caught cetaceans, depending on the identity of one specimen that was not identified to the species

Table 6. Estimates of entanglement (P_{ent} × LH) and mortality of harbour porpoise using license holder (LH) data.

				Mortality	
Salmon area	No. of LH	Estimated entanglement	Estimated mortality	LCL	UCL
2004					
C	716	10.88	5		
D	288	4.38	2		
E	395	6.00	3		
Total		21	10	5	18
2005					
C	715	10.87	5		
D	293	4.45	2		
E	381	5.79	3		
Total		21	10	5	18

Note: LCL, lower confidence limit; UCL, upper confidence limit.

Table 7. Estimates of harbour porpoise mortality in British Columbia's south coast.

Year	Our estimate: all small cetaceans	NMFS 2006: harbour porpoise only	USA and Canadian waters combined
2004	40	15	55
2005	24	15	39

level (Hall et al. 2002). As a result, our estimate of total mortality of all small cetacean species would be in the range of 23 to 36 animals using this method. It is important to note that in any given year, fewer license holders actually fish than are registered (L. Keary, Fisheries and Oceans Canada, 3225 Stephenson Point Road, Nanaimo, BC V9T 1K3, Canada, personal communication). However, not all license holders fish equal amounts throughout any given salmon season. We present these results for illustrative purposes and to draw attention to the very preliminary nature of existing data on current estimates of fishery-related mortality. Neither the observer data nor the license holder data alone can give a robust estimate of current levels of small cetacean mortality in BC gillnet fisheries.

Transboundary implications

According to the 2006 Stock Status Report for Inland Waters of Washington, excluding the proportion of animals expected to be in Canadian waters, the estimated size of the harbour porpoise population in inland Washington waters is N = 10 682 (CV = 0.38) when corrected for availability and perception bias (NMFS 2006). This is an average from the 2002 and 2003 population estimates (NMFS 2006). The minimum population estimate, using the lower 20th percentile of a lognormal distribution, is 7841 animals (NMFS 2006). The PBR is then 63 harbour porpoise per year the using 4% default value for R_{max} and a recovery factor of 0.4 (NMFS 2006). The minimum estimated fishery-related mortality and serious injury in US waters is 15.2 harbour porpoise per year (NMFS 2006). Transboundary totals based on the BC observer data extrapolations and the US reported mortality estimates are presented (Table 7; NMFS 2006).

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It should be noted that harbour porpoise likely only comprise some proportion of the total small cetacean bycatch for our south coast estimates. However, even if our small cetacean estimates represent only harbour porpoise, the combined estimates fall within our calculated mortality limits for both objectives from MMPA (ML = 223–447; Table 2) and ASCOBANS (ML = 89–178; Table 2) frameworks based on the $g(0) = 1$ and $g(0) = 0.5$ assumptions.

Discussion

The calculations presented in this paper represent a first attempt to assess sustainable limits to anthropogenic mortality for small cetaceans in BC coastal waters and are of use as Canadian policy makers develop quantitative triggers for conservation and management and estimates of allowable harm for marine mammals (Hammill and Stenson 2007; Johnston et al. 2000). The proposed limits are preliminary because we have relatively imprecise abundance estimates, no empirical estimate of the bias in our abundance estimates (although a range of likely values are considered from those reported in the literature), and incomplete fishery coverage to estimate bycatch rates. Given the preliminary nature of the estimated rates of bycatch, definitive conclusions about the current impacts of the commercial salmon gillnet fishery in BC on small cetacean populations would be premature. It is worth noting that some attributes of the BC selective salmon gillnet fishery as it is currently practiced might lead to lower bycatch and mortality rates than might otherwise be expected. For example, BC gillnet fishery openings tend to be spatially and temporally limited. Openings are relatively short (on the order of days, rather than weeks or months), and vessels generally remain in the vicinity of their nets, thereby allowing for a prompt response to any observed entanglement event. Generally, it is reasonable to state that the extent to which small cetaceans use the specific regions targeted by fisheries is not well studied in BC.

One parameter that has large potential to influence our results and interpretation is the live-release rate of approximately 50% that we use (Hall et al. 2002). Hall et al. (2002) noted that observers in their study monitored four entanglement events, two of which resulted in live release. The authors further noted that license holders described the release of 10 of 19 (52.6%) harbour porpoise entangled in gill nets. High live-release rates are known from dedicated and labour-intensive programs in which responders remove porpoise that have become entrapped in herring weirs (reviewed in NMFS 2006), but this is certainly the exception to the rule. Studies of entangled porpoise refer to "surface drop-outs" (Trippel et al. 1996) to describe cases when porpoise carcasses have become disentangled from gear as it is being retrieved — but clearly, the findings of Hall et al. (2002) suggest that entanglement does not necessarily always lead to mortality. This preliminary result may be a reflection of small sample sizes, or the estimate from the observers may be biased because of atypical efforts on the part of fishermen to reduce porpoise mortality while the fishery is being observed. Alternatively, live releases may be inherent to this particular fishery in that the selective gear is generally attended, and indeed, both methods to estimate live-release rate resulted in similarly high values (Hall et al. 2002). Of course, net entanglement is likely a very stressful event for small cetaceans, and disentangled animals may die shortly after release. Directed studies to follow postrelease survivorship are needed, especially if conventional fishing practices in BC salmon gillnet fisheries can yield information that may increase the live-release rate in other fisheries.

On a finer scale, it must be noted that the observer data P_{ent} determined by Hall et al. (2002) is based solely on the south coast fishery. No comparable estimate of P_{ent} exists for the north coast waters, and as such we assumed that P_{ent} was applicable coast-wide. While the mortality limits themselves are highly reliant on the quality and quantity of data we have available for input, we see value in the approach used here.

Notwithstanding these caveats, a few key results emerge from this exercise. First, our best estimates of coast-wide bycatch levels in 2004 and 2005 were in the range of the MLs we calculated, and thus, were potentially of concern for harbour and Dall's porpoises if (*i*) Canada's management objectives were as precautionary as those under ASCOBANS or MMPA and (*ii*) current estimates of porpoise abundance were unbiased (Williams and Thomas 2007). Bycatch mortality was more likely to be exceeding ML for these species if the fraction of bycatch for which species identity is uncertain is composed of porpoise rather than dolphins. In contrast, almost no scenario that we considered makes it likely for current salmon gillnet fishing in BC coastal waters to be posing an unacceptable risk to Pacific white-sided dolphins at the population level. Fishing activities could be having a variety of sublethal impacts on dolphins and other cetaceans that are not considered here. Previous analyses have found that even low levels of clustered removals of key individuals in highly social odontocetes can result in fragmentation of social networks, which could lead to fitness-level effects (Williams and Lusseau 2006). Temporary habitat degradation associated with commercial fishing activities in this region has been linked to changes in killer whale feeding behaviour, habitat use, energetics, and activity budgets (Williams et al. 2006).

It should also be noted that while BC gillnet fisheries do cause anthropogenic mortality, numbers of bycaught porpoise were generally low compared with other regions. In the 2002 nearshore gillnet cod fishery in Newfoundland waters, Lawson et al. (2004) estimated that bycatch of small cetaceans, nearly all of which were harbour porpoise, was likely to be in the low thousands. Lesage et al. (2006) used similar methods to Hall et al. (2002), combining questionnaire surveys and at-sea observer programs to estimate incidental catch of harbour porpoises in the gillnet fishery of the Estuary and Gulf of St. Lawrence. Total bycatch in that region in 2000 and 2001 was estimated by the authors' preferred method to be in the low thousands. In contrast, most scenarios that we considered provided estimates of total harbour porpoise bycatch in BC coastal gillnet fisheries in the low hundreds. While bycatch may be an order of magnitude lower in BC fisheries than in east coast counterparts, so too does porpoise abundance appear to be lower in west coast waters (Lawson et al. 2004, Lesage et al. 2006, Williams and Thomas 2007). As a result, porpoise bycatch may be problematic in all three management areas. Improved ob-

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server coverage is required in all three areas to refine entanglement rates, to reduce uncertainty, and to accurately assess whether current levels of anthropogenic mortality actually fall within our best estimates of sustainable limits. The possibility that PBR levels are reached or exceeded increases with data uncertainty.

One priority area for future field research should be to estimate g(0) directly for harbour and Dall's porpoise for ongoing shipboard sightings surveys, to assess how much bias actually exists in current estimates of abundance. A second priority will be to estimate seasonal variability in animal abundance. Third, mortality limits such as these are intended to be applied to panmictic population units (i.e., populations in which all individuals mix and interbreed freely). Applying these limits to larger units risks not achieving the objective for a distinct subunit if that subunit experiences a disproportionate amount of the bycatch (Wade 1998). Consequently, there is a need for better understanding of population structure in all three species. If small or restricted dolphin or porpoise populations exist in BC, a localized conservation concern may exist.

In terms of monitoring fisheries-related mortality, an obvious priority is the need for increased funding for fishery observer programs that include greater spatial and temporal coverage and adequate training in species identification of marine mammals. Our work highlights the need for accurate, consistent, and long-term monitoring of all fisheries that have the potential to affect marine mammals. Evaluation of the harbour porpoise bycatch-related mortality in the Bay of Fundy was, in part, facilitated with on-board observers that covered between 2.3% and 100% of vessel trips throughout the 1993–1994 fishing season (Trippel et al. 1996).

We note that Canada is currently in the process of developing quantitative conservation objectives based on the precautionary approach (Hammill and Stenson 2007) and calculating quantitative mortality limits for some marine mammal stocks, but also that no generic procedures have yet been made publicly available for application to all marine mammal stocks. In our view, one of the strengths of Canada's Species at Risk Act is its requirement that the "best available knowledge" be used to define objectives in recovery strategies. In that spirit, our first attempts to estimate mortality limits using the best available data, however sparse, are an important first step toward assessing the sustainability of fisheries bycatch for small cetacean species in Canada's Pacific region. This process has helped to identify data shortcomings, which, once addressed, may allow more rigorous analyses in future. We hope that the approach outlined here may provide a step in the right direction for the conservation of other data-poor species, which include many that are of little or no commercial value.

By design, PBR is a simple strategy for achieving management objectives with regard to anthropogenic mortality. PBR provides a maximum mortality, below which one would expect to achieve management objectives with respect to population status in the long term. The only data requirement of the procedure is an estimate of current abundance, which is updated with some frequency over time. For populations about which there are very few data, PBR is often implemented by setting most parameters (eqs. 1 and 2) to default values and the recovery factor (F) is used to adjust the performance of the procedure so that it is robust to uncertainty in estimates of population size, mortality, and current population status relative to K (Wade 1998). There are very few data available on the status and dynamics of small cetacean populations in our study area. Therefore, we accepted default PBR parameter values and conducted simulations to determine values for the recovery factor that would ensure our proposed management objectives would be achieved given the uncertainty in abundance, mortality, and population status.

In addition to the PBR approach, there are numerous alternative management strategies and procedures that can be taken with regard to managing anthropogenic removals from a population. For example, the International Whaling Commission has developed an algorithm for setting catch limits as part of its Revised Management Procedure (Cooke 1999). A more data-intensive approach is to conduct a population assessment to derive estimates or probability distributions for quantities of interest to management like population size, status, and dynamics (e.g., Hoyle and Maunder 2004). Mortality limits can then be set as some function of these estimates or distributions. Furthermore, these probability distributions can be used as a basis for simulations to test the performance of a management procedure and lend themselves easily to risk assessment and decision analysis techniques. Unfortunately, the data required to conduct such an assessment for small cetacean populations in BC do not currently exist and are not likely to exist in the near future. In the meantime, PBR is a simple management procedure that can be used until a more in-depth assessment can be conducted.

In general, there are large uncertainties involved in the estimation of the dynamics and status of marine mammal populations. For example, even given adequate funding, it is difficult to detect trends in abundance of marine mammal populations (Taylor et al. 2007). Management strategies that rely only on the detection of a statistically significant population decline risk only enacting necessary management measures once it is too late. Similarly, management triggers that rely only on point estimates of population size or status without consideration of the confidence intervals associated with those estimates engender high risk in the face of uncertainty. Management procedures such as PBR can be tested and tuned through simulation to ensure that they are robust to uncertainty and inherently minimize the risk that management objectives will not be met.

Much of fishery management centres on species from which economic gain is expected. Species not considered valuable, because they have no harvest value or are caught incidentally to those with harvest value, tend to be less well studied until some survival risk is determined. As part of a conservation framework in Canada, the Species at Risk Act provides guidance for compilation and evaluation of the best available science by COSEWIC. However, at this stage in the implementation of the legislation there is no mandate for providing the resources necessary to fill in data gaps for species where survival risk is a concern. In this sense, we see strong value for the implicit reward for science under the PBR approach (Wade 1998). In the PBR approach, the main reward is that more precise survey and bycatch estimates would likely allow higher, more appropriate mortality

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limits, which in turn would carry lower economic costs to those fisheries responsible for reducing bycatch. A similar reward-for-science framework would fit well within the overarching mandate of Fisheries and Oceans Canada, which "...includes responsibility for the conservation and sustainable use of Canada's fisheries resources while continuing to provide safe, effective and environmentally sound marine services that are responsive to the needs of Canadians in a global economy" (Fisheries and Oceans Canada Web site: www.dfo-mpo.gc.ca/us-nous_e.htm).

Quantitative management objectives will also facilitate species-specific, cross-border comparisons and cooperation, so that managers in Canada and the USA can better fulfil their respective mandates and reduce the risk to species whose numbers are threatened by current fishing practices in both countries. Common currency in terms of quantitative management objectives will also provide a better understanding of how management actions in one country can impact populations that spend time in the territorial waters of the adjacent country. Though addressing these topics may seem unwieldy, recent international cooperation between Canada and the US on the conservation and recovery of resident killer whales (*Orcinus orca*) indicates that transboundary, international cooperation and conservation of an endangered species is possible (Resident Killer Whale Recovery Team 2007). Indeed, although the two countries have treaties for exploited species (e.g., the Pacific Salmon Treaty from 1985 — www.psc.org/publications_psctreaty.htm; the Pacific Halibut Treaty from 1923 — www.iphc.washington.edu/HALCOM/history/1923can.htm), informal cooperation between the two countries on conservation of at-risk species that are subject only to nonconsumptive use may prove to be more successful.

If a management objective is to maintain a population at a certain level of its true, natural equilibrium size, then assessments of whether mortality limits are being exceeded should incorporate all known sources of anthropogenic mortality. In this study, we restricted our discussion to bycatch in commercial gillnet fisheries. But a similar approach can be used to assess whether any source of anthropogenic mortality is potentially problematic. Additional sources of mortality could include, for example, ship strikes, entanglement in antipredator nets around fish farms, intense acoustic trauma, or oil spills.

While our results are preliminary and hindered by currently small sample sizes and low statistical power, the approach we outline offers a quantitative and precautionary framework for Canada to meet its management objectives to maintain favourable conservation status of small cetacean populations. We also hope that our work can serve as a basis for transboundary evaluation of the status of (and threats to conservation of) small cetaceans in BC and Washington, where transboundary cooperation has greatly influenced the conservation of resident killer whale populations in recent years.

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Extending the von Bertalanffy growth model using explanatory variables

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Abstract: von Bertalanffy parameters are usually estimated for a species, perhaps by sex, in some well-defined geographical area. An alternative way to estimate von Bertalanffy parameters is to model them in a general fixed-effects nonlinear model. For this model, the length of the *i*th individual is modeled as $y_i = f(\Theta, t_i, x_i) + \varepsilon_i$, where y_i is the length and t_i is the age of the *i*th specimen at the time of sampling, Θ are the unknown parameters required to model von Bertalanffy growth, and x_i are covariates associated with the *i*th specimen that minimally contain sex information (x_{i1}), but may also contain additional covariates. Standard nonlinear least squares and associated likelihood methods can be used to estimate parameters for this model. For Pacific ocean perch (*Sebastes alutus*), we model the effect that depth of collection has on estimated von Bertalanffy growth parameters; for sablefish (*Anoplopoma fimbria*), we model the effects due to latitude of collection; and for walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea, we model the effects due to variations in year classes. Results illustrate how modeling von Bertalanffy growth parameters directly using explanatory variables can be used to describe how growth relates to geographic, environmental, or biological factors.

Résumé : On estime généralement les paramètres de von Bertalanffy pour une espèce, parfois pour chacun des sexes, dans une région géographique bien définie. Une méthode de rechange pour estimer les paramètres de von Bertalanffy est de les modéliser dans un modèle linéaire général à effets fixes. Dans ce modèle, la longueur du *i*ième individu est calculée d'après $y_i = f(\Theta, t_i, x_i) + \varepsilon_i$, dans lequel y_i est la longueur et t_i est l'âge du *i*ième individu au moment de l'échantillonnage, Θ les paramètres inconnus nécessaires pour modéliser la croissance de von Bertalanffy et x_i les covariables associées au *i*ième individu qui contiennent au minimum de l'information sur son sexe (x_{i1}), mais qui peuvent aussi comprendre d'autres covariables. La méthode standard non linéaire des moindres carrés et les méthodes associées de vraisemblance peuvent servir à estimer les paramètres de ce modèle. Chez le sébaste à longue mâchoire (*Sebastes alutus*), nous modélisons l'effet de la profondeur de la récolte sur les paramètres estimés de croissance de von Bertalanffy; chez la morue charbonnière (*Anoplopoma fimbria*), nous modélisons les effets causés par la latitude de la récolte; finalement, chez la goberge de l'Alaska (*Theragra chalcogramma*) dans l'est de la mer de Béring, nous modélisons les effets dus aux variations dans les classes d'âge. Ces résultats montrent comment la modélisation directe des paramètres de croissance de von Bertalanffy à l'aide de variables explicatives peut servir à décrire comment la croissance est reliée aux facteurs géographiques, environnementaux et biologiques.

[Traduit par la Rédaction]

Introduction

The von Bertalanffy growth curve (von Bertalanffy 1938) is perhaps the most widely used model in fisheries science and has been particularly useful in describing growth for many varieties of stock assessment models (Deriso 1980; Methot 1990; Quinn and Deriso 1999). Values of growth parameters have also been intimately linked to natural mortality rates (Beverton and Holt 1956; Pauly 1980; Vetter 1988).

It has usually been the case that von Bertalanffy growth parameters are considered population parameters, and parameters are most often estimated from sampled length-at-age data using nonlinear least squares (Allen 1966; Kimura 1980; Seber and Wild 1989). However, this paradigm is questionable in the context of tag-recapture data, where it is natural to consider growth on an individual fish basis. In this context, a theory of von Bertalanffy growth wherein individual fish can have different von Bertalanffy growth parameters has evolved (Sainsbury 1980; Kirkwood 1983; James 1991). Here, individual growth parameters are thought to have a random component beyond that of the population average.

We extend this concept further by allowing individual fish growth to include a nonrandom component, which is dependent on sampling covariates (i.e., depth or latitude of sampling) or a more detailed population partition (i.e., year classes). Fitting such models summarizes information by functionally relating population parameters to covariates. Conceptually, this can also be thought of as placing each fish in a population stratum that is not necessarily based on area and then estimating parameters for that stratum. Regional population parameters, should they be necessary, can then be estimated by averaging the population parameters for individuals sampled from a particular region. This provides a way of comparing von Bertalanffy parameter estimates from arbitrarily small or large regions.

The main problem in applying this type of method is to have an adequate sampling of the population of interest, us-

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Table 1. Sum of squared residuals (SSR) and the information theoretical criterion (AIC) for different stages in fitting the EVB model fits.

Species	Model description	Sample size (n)	No. of parameters (p)	SSR	AIC
Pacific ocean perch	Without sex	16 182	3	109 477	76 865
	With sex	16 182	6	103 127	75 905
	With sex and depth	16 182	9	101 822	75 704
Sablefish	Without sex	31 870	3	1 858 112	220 021
	With sex	31 870	6	1 488 835	212 966
	With sex and latitude	31 870	9	1 077 616	202 670
Walleye pollock	Without sex	36 750	3	1 082 065	228 604
	With sex	36 750	6	1 040 633	227 176
	With sex and year classes	36 750	45	979 213	225 018
	With sex and year-class strength	36 750	9	1 038 199	227 096

Note: Results show improved model fits as further information are added to the models, with no indication that the models are overparameterized. For modeling walleye pollock, year class refers to year class entered as dummy variables, and year-class strength refers to regression directly on the number of 1-year-olds in the year class. Pacific ocean perch, *Sebastes alutus*; sablefish, *Anoplopoma fimbria*; walleye pollock, *Theragra chalcogramma*.

ing consistent ageing criteria, so that all parameters can be successfully estimated. We have picked three species that have been regularly aged at the Alaska Fisheries Science Center (AFSC) since 1982 using a combination of otolith surface and cut-and-burn ageing methods (Kimura and Anderl 2005). Although ageing methods may have changed somewhat, especially during the earlier years, ageing methodologies for these species are believed to have been fairly stable. Using Pacific ocean perch (*Sebastes alutus*), we model the effect that depth of collection has on estimated von Bertalanffy growth parameters; using sablefish (*Anoplopoma fimbria*), we model the effects due to latitude of collection; and using walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea, we model the growth effects of individual year classes. It is important to realize that adequate sampling goes beyond simply having a large sample size. In addition, samples need to be stratified so that modeled effects are likely to be real, rather than the result of, for example, an artifact of inadequate age ranges associated with the explanatory variables.

Mathematically, we model parameters as linear in the explanatory variables, although the von Bertalanffy function overall is decidedly nonlinear. This is similar to the approaches used in generalized linear models (McCullagh and Nelder 1989) and in the nonlinear mixed model (Lindstrom and Bates 1990).

Kimura (1980, 1990) describes how least squares estimation is intimately linked to both maximum likelihood under the normal error assumption and the usual F test for testing significance of effects. Furthermore, viewed as a normal likelihood, the minimum information theoretical criterion (AIC; Akaike 1974) can be used to select parsimonious models under the class of models being considered.

Materials and methods

Statistical methods

In this paper, the von Bertalanffy parameters enter into the growth equation in the usual way. However, unlike the usual representation, the parameters can vary for individual fish (i.e., $\{L_\infty, K, t_0\}$) due to the influence of covariates. The von Bertalanffy model representation for the ith fish is therefore as follows:

$$y_i = L_{\infty,i}(1 - \exp(-K_i(t_i - t_{0i})))$$

where y_i and t_i are the length (cm) and age (years), respectively. In this paper, $\{L_\infty, K, t_0\}$ will be estimated on the logarithmic scale, therefore they need to be exponentiated before being substituted into the von Bertalanffy curve and the sum of squared residuals (SSR) calculated.

Expanding this representation to include all parameters, covariates, and an error term, the length of the ith individual becomes $y_i = f(\phi, t_i, x_i) + \varepsilon_i$, where ϕ are the unknown parameters required to model von Bertalanffy growth, and x_i are covariates associated with the specimen of length y_i, which minimally contains the sex $\{x_{i1}\}$, but may also contain such information as depth of capture, latitude of capture, or the year class to which the ith individual belongs. Here, ε_i is the usual normally distributed error term. In our examples, the covariates for sex and year classes are "dummy variables", as used by Draper and Smith (1981), and regression variables (i.e., depth and latitude), which are logarithms of decimalized values.

To be more specific, let $\phi' = \{\beta_{0L}, \beta_{0K}, \beta_{0t}, \beta_{1L}, \beta_{1K}, \beta_{1t}, \beta_{2L}, \beta_{2K}, \beta_{2t}, \ldots, \beta_{qL}, \beta_{qK}, \beta_{qt}\}$, where we assume that there are q covariates. The interpretation of ϕ in terms of the von Bertalanffy parameters for one specimen makes the parameterization quite transparent. Often it will be desirable to estimate the von Bertalanffy parameters on the logarithmic scale (we use only natural logs in this paper):

$$\log\begin{pmatrix} L_{\infty,i} \\ K_i \\ t_{0i} + 10 \end{pmatrix} = \begin{pmatrix} \beta_{0L} + x_{i1}\beta_{1L} + \ldots + x_{iq}\beta_{qL} \\ \beta_{0K} + x_{i1}\beta_{1K} + \ldots + x_{iq}\beta_{qK} \\ \beta_{0t} + x_{i1}\beta_{1t} + \ldots + x_{iq}\beta_{qt} \end{pmatrix}$$

The reason that 10 is added to t_{0i} is that the log of negative values of t_{0i} is not possible. Therefore we simply estimate $t_{0i} + 10$, but subtract 10 before evaluating the von Bertalanffy function and calculating the SSR. Compared with parameters on the original scale, these parameters on the logarithmic scale are more easily understood by reparameterizing the intercept values as $\beta_{0L} = \log(L_\infty^0)$,

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Fig. 1. Histograms for Pacific ocean perch (*Sebastes alutus*) age–length data showing (*a*) year of collection, (*b*) depth of collection, (*c*) specimen ages, and (*d*) year classes.

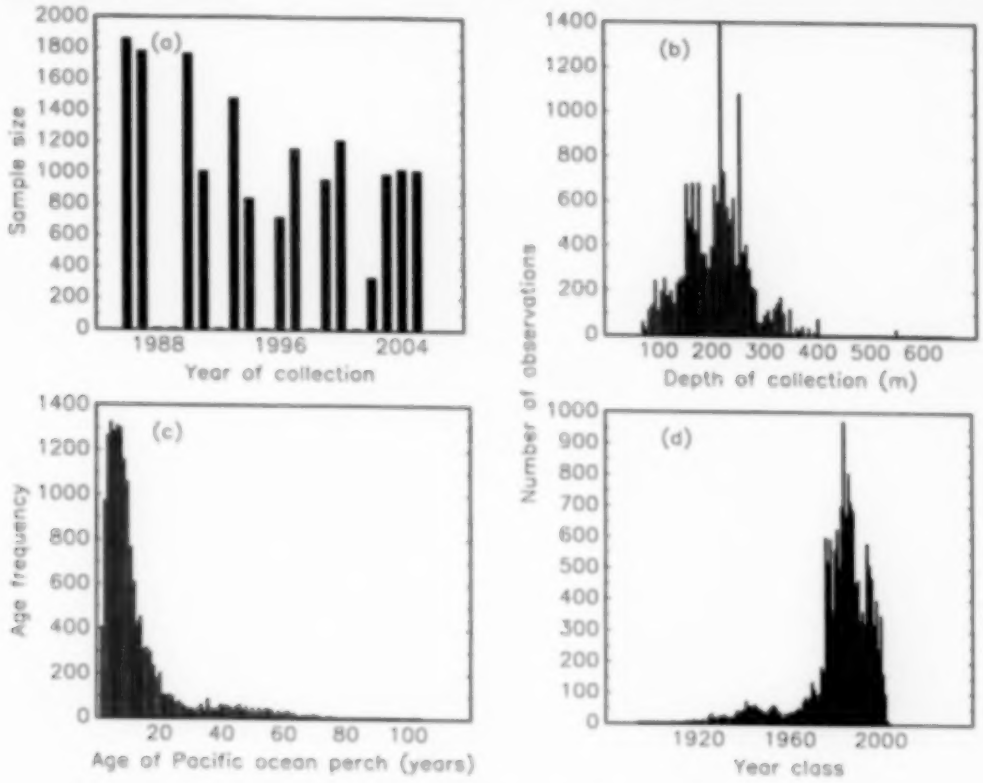

Table 2. Parameter estimates from fitting the EVB model, with bottom depth, to Pacific ocean perch (*Sebastes alutus*) data from the Aleutian Islands and Gulf of Alaska regions.

Type	Parameter	Estimates	SE(Est.)	CV(Est.)	*t* value	*P* value
Constant	β_{0L}	3.93651	0.02523	0.00641	155.99802	0.00001
	β_{0K}	−2.00884	0.10880	−0.05416	−18.46323	0.00001
	β_{0t}	2.16975	0.04538	0.02092	47.81035	0.00001
Sex	β_{1L}	0.06464	0.00240	0.03706	26.98509	0.00001
	β_{1K}	−0.11320	0.01246	−0.11011	−9.08161	0.00001
	β_{1t}	−0.00364	0.00574	−1.57751	−0.63391	0.52615
log(depth)	β_{2L}	−0.04537	0.00463	−0.10201	−9.80341	0.00001
	β_{2K}	0.05795	0.02047	0.35322	2.83113	0.00464
	β_{2t}	0.01516	0.00882	0.58166	1.71922	0.08559

Note: Degrees of freedom (df) for the *t* value is 16 173; SE(Est.), standard error of the estimate; CV(Est.), coefficient of variation of the estimate.

$\beta_{0K} = \log(K^0)$, and $\beta_{0t} = \log(t_0^0)$. Notice that the additive model on the logarithmic scale becomes multiplicative on the original scale. For example, the $L_{\infty i}$ term becomes $L_{\infty i} = L_\infty^0 \exp(x_{i1}\beta_{1L} + \ldots + x_{ip}\beta_{pL})$ on the original scale. For this reason, we estimate the influence on von Bertalanffy parameters of various explanatory variables as exponential terms such as $\exp(x_{ij}\beta_{jL})$, which we call multipliers, where greater values imply increased parameter values.

There are two well-known advantages of estimating parameters on the logarithmic scale. First, even parameters differing greatly in magnitude on the original scale are nearly the same magnitude on the logarithmic scale, making estimation computationally easier; and second, von Bertalanffy parameters L_∞ and K will be constrained to be positive on the original scale. Negative K parameter estimates can be a serious problem when fitting von Bertalanffy parameters when model residuals are large. Because t_0 will also be constrained in the estimation to be positive, even though it, in fact, may be negative, $\tilde{t}_0 = t_0 + 10$ should be estimated rather than t_0. As already pointed out, the bias of 10 can be subtracted before evaluating von Bertalanffy growth parameters on the original scale, allowing $\hat{t}_0 = \hat{\tilde{t}}_0 -$

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10 to be negative. Although this may not appear elegant, in fact, it is more elegant in describing the statistical theory and estimating variances. It appears that all of the methods available for modeling fixed effects, e.g., dummy variables, interactions, contrasts, etc., can be used in the context of this model.

Adding a three-dimensional random effect to this model leads to the nonlinear mixed-effects model (Lindstrom and Bates 1990). The nonlinear mixed model seems most appropriate in the context of repeated measure, and Schaalje et al. (2002) used this method to analyze backcalculated growth data. However, in this paper, we are interested only in the simpler fixed-effects model, which seems appropriate for measuring overall population effects.

Regardless of how the von Bertalanffy parameters are themselves parameterized, the sum of squared residuals on which the estimation is based is on the original nontransformed scale $\mathrm{SSR} = \sum_i (y_i - \hat{y}_i)^2$, where y_i is the observed length (cm) and $\hat{y}_i$ is the predicted length (cm) from the von Bertalanffy growth function. Assuming that the $\{\varepsilon_i\}$ are independent and normally distributed, minimizing SSR will provide maximum likelihood estimates (Kimura 1980). The covariance matrix of $\hat{\phi}$ is estimated using the gradient function $Z = \{z_{ij}\}$, where $z_{ij} = \partial y_i / \partial \phi_j$. Here, ϕ_j represents the jth entry of ϕ. The gradient approximation to the covariance matrix (Kimura 1980; Press et al. 1986) is $\Sigma(\hat{\phi}) = s^2(Z'Z)^{-1}$, where $s^2 = \sum_i (y_i - \hat{y}_i)^2 / (n - 3(q+1))$ and n is the total number of $\{y_i, t_i\}$ observations.

When regressing on continuous covariates, a more subtle issue arises concerning parameter estimation on the logarithmic scale. If von Bertalanffy parameters are estimated on the logarithmic scale, then linear influences with covariates on a nonlogarithmic scale will tend to be overwhelming, so that the β estimates will be forced towards zero. Alternatively, if covariates are logarithmically transformed prior to estimating effects, a curvature is introduced into the relationship between the von Bertalanffy parameters and the covariate. If one is willing to live with this curvature, the advantages are great in fitting parameters on the logarithmic scale and logarithmically transforming the covariates. This is the approach that we use in this paper. Note also that the logarithmic transformation does not apply to dummy variables such as the ones we used in the parameterization of sex and year-class effects.

We found that fitting these models in stages allowed for stable and trouble-free estimation. We started with a single von Bertalanffy fit to all of the data with parameters on the nonlogged scale and took the logs of these values as initial estimates of $\beta_{01}, \beta_{02}, \beta_{03}$. We then added the sex effect and refit the model. We then added whatever explanatory variables interested us and performed a final fit to the model, with all parameters on the logarithmic scale. This algorithm was programmed in the Gauss computer language (Aptech Systems, Inc. 1996), using their OPTMUM function minimizer.

Least squares, likelihood, *F* test, and the AIC criterion

The nonlinear least squares method used to estimate parameters (i.e., minimizing SSR) is equivalent to maximizing the log-likelihood under the assumption of independent, normally distributed errors (Kimura 1980). The F test used to test the significance of the model covariates in this paper is a monotone transformation (Kimura 1990) of the likelihood ratio test described in Kimura (1980), and therefore they are equivalent. The likelihood ratio test that is considered tests the significance of the model including covariates against the model that includes only the constant and sex parameters, which meets the nesting requirements of the likelihood ratio test. The fact that the F test using the extra sum of squares principal (Draper and Smith 1981) is equivalent to the likelihood ratio test often goes unnoticed, even though it unifies and simplifies the likelihood theory surrounding nonlinear least squares. Let SSR_1 and SSR_2 and p_1 and p_2 represent the sum of squared residuals and number of parameters in the model without and with covariates, respectively. Then under the null hypothesis that the covariates have no effect on von Bertalanffy growth parameters, the statistic $F = [(\mathrm{SSR}_1 - \mathrm{SSR}_2)/(p_2 - p_1)]/[\mathrm{SSR}_2/(n - p_2)]$ has an F distribution with df $= p_2 - p_1, n - p_2$ degrees of freedom, where n is the total sample size.

Akaike (1974) derived a measure of goodness of fit that takes into account the number of parameters independently estimated in the model. Using the minimum information theoretical criterion (AIC), it is possible to assure that the selected model provides a parsimonious explanation of the data. Because the standard nonlinear least-squares fit pro-

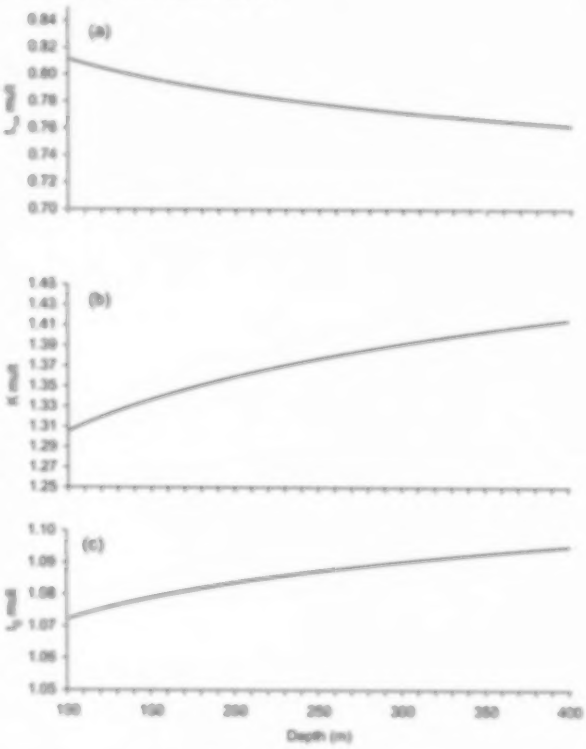

Fig. 2. Modeled von Bertalanffy growth parameter multipliers, $\exp(x_2\beta_{i2})$, estimated from the Pacific ocean perch (*Sebastes alutus*) EVB depth model, that describe the effect that log(depth), x_2, has on (*a*) L_∞, (*b*) K, and (*c*) t_0.

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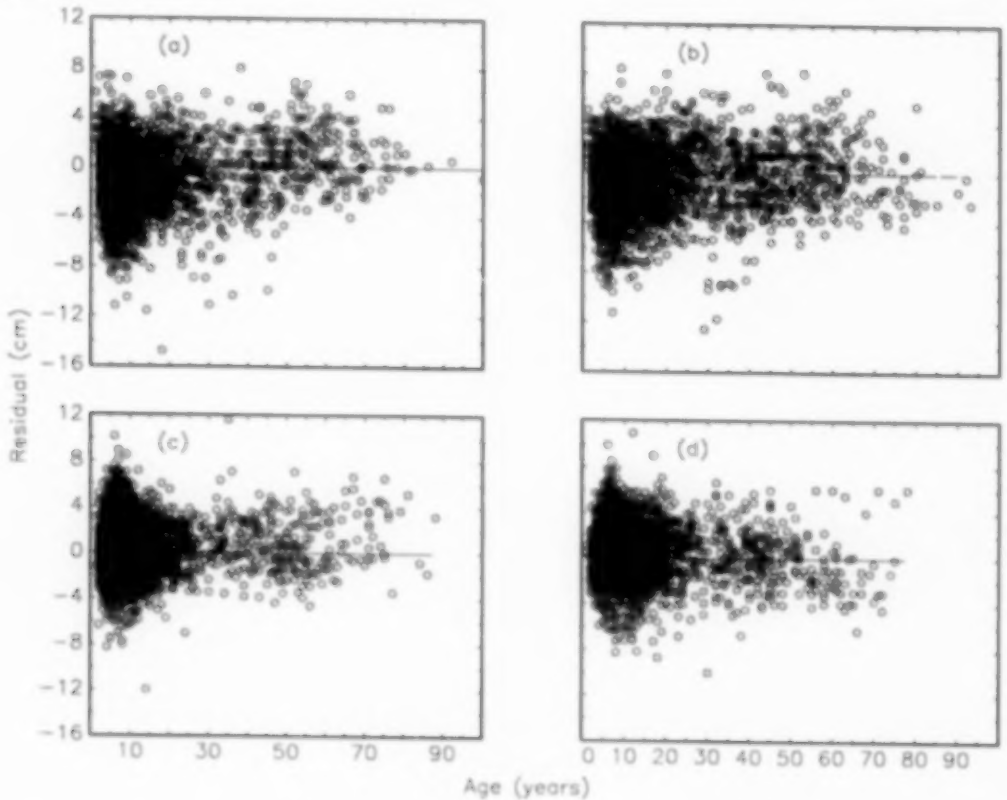
Table 3. Comparison of regional von Bertalanffy parameter estimates for Pacific ocean perch (*Sebastes alutus*) using the SVB and EVB models.

Estimate	Region	Sex	L_∞	K	t_0	SE(L_∞)	SE(K)	SE(t_0)	SSR
SVB	AI	Male	39.836	0.165	–0.753	0.095	0.002	0.058	21 328
		Female	42.756	0.148	–0.711	0.094	0.002	0.055	24 197
	GOA	Male	40.283	0.199	–0.408	0.089	0.002	0.046	21 299
		Female	42.590	0.179	–0.471	0.097	0.002	0.049	23 674
EVB	AI	Male	40.239	0.183	–0.507	0.074	0.002	0.045	25 012
		Female	42.898	0.163	–0.540	0.075	0.001	0.043	27 631
	GOA	Male	40.363	0.182	–0.517	0.079	0.002	0.043	23 499
		Female	43.003	0.163	–0.548	0.079	0.001	0.042	25 680

Note: SE, standard error; SSR, residual sum of squares. Regions: AI, Aleutian Islands; GOA, Gulf of Alaska.

Fig. 3. Residual plots calculated from the Pacific ocean perch (*Sebastes alutus*) EVB depth model fits with fish age along the x axis. Data are stratified by region (Aleutian Islands (AI), Gulf of Alaska (GOA)) and sex (males, females): (*a*) AI males, (*b*) AI females, (*c*) GOA males, and (*d*) GOA females.



vides maximum likelihood estimates under the assumption of normal errors, assuming a normal likelihood model provides a natural link between nonlinear least squares and the AIC goodness of fit criterion.

The maximum of the log-likelihood can be expressed as

$$L = -(n/2)\left(1 + \log(2\pi \mathrm{SSR}/n)\right)$$

where SSR is the minimum residual sum of squares and n is the total sample used for fitting (i.e., not the degrees of freedom). Substituting L into the AIC formula we obtain:

$$\mathrm{AIC} = n(1 + \log(2\pi\ \mathrm{SSR}/n)) + 2p$$

where p is the number of parameters being estimated in the nonlinear least squares. The best fitting model should minimize this value of AIC. If adding parameters increases the value of AIC, then the explanatory model is not parsimonious.

Model specification

Parameterizing different growth between sexes

As mention earlier, we use the first covariate in x_i as a

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Fig. 4. Histograms for sablefish (*Anoplopoma fimbria*) age–length data, showing (*a*) year of collection, (*b*) latitude of collection, (*c*) specimen ages, and (*d*) year classes.

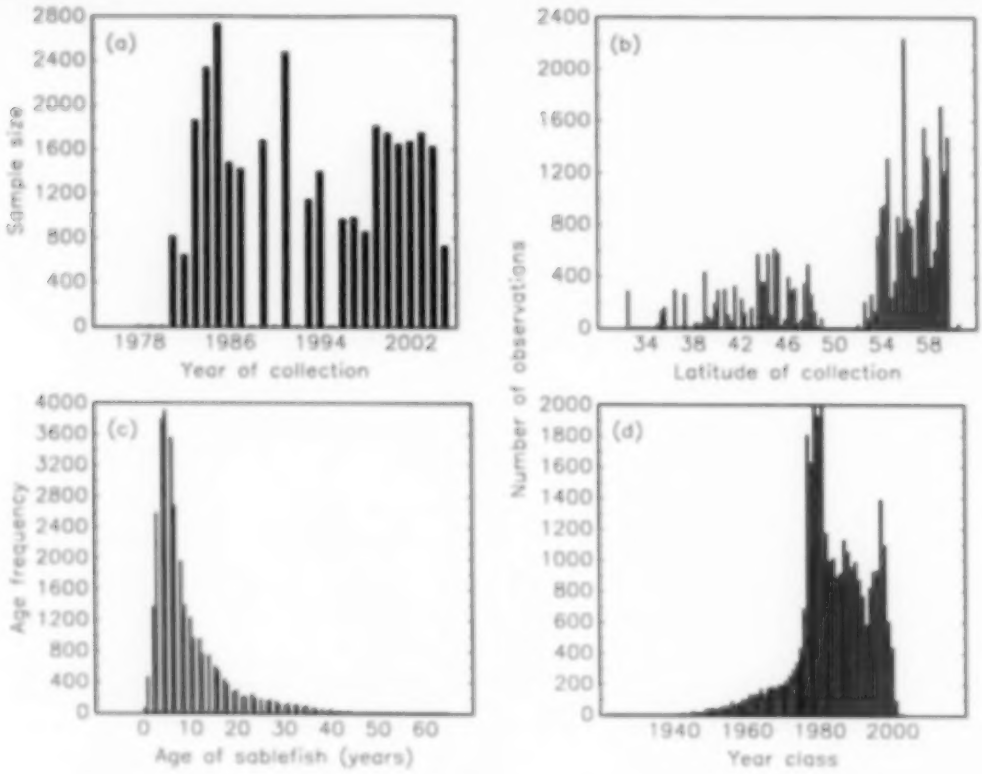

Table 4. Parameter estimates from fitting the EVB model, with latitude (lat), to sablefish (*Anoplopoma fimbria*) data collected along the US West Coast and Gulf of Alaska regions.

Type	Parameter	Estimates	SE(Est.)	CV(Est.)	*t* value	*P* value
Constant	β_{0L}	1.94000	0.02988	0.01540	64.92671	0.00001
	β_{0K}	0.72044	0.26255	0.36443	2.74399	0.00607
	β_{0t}	1.47124	0.15873	0.10789	9.26882	0.00001
Sex	β_{1L}	0.17334	0.00223	0.01288	77.65227	0.00001
	β_{1K}	−0.27685	0.01979	−0.07149	−13.98814	0.00001
	β_{1t}	0.00407	0.01212	2.97444	0.33620	0.73672
log(lat)	β_{2L}	0.56445	0.00750	0.01329	75.24297	0.00001
	β_{2K}	−0.49897	0.06660	−0.13348	−7.49193	0.00001
	β_{2t}	0.14901	0.04061	0.27255	3.66912	0.00024

Note: Degrees of freedom (df) for the *t* value is 31 861. SE(Est.), standard error of the estimate; CV(Est.), coefficient of variation of the estimate.

dummy variable indicating sex. For males, we set $x_{i1} = 0$ and for females we set $x_{i1} = 1$, so that when there are no other covariates, we have

$$\log\begin{pmatrix} L_{\infty i} \\ K_i \\ t_{0i} + 10 \end{pmatrix} = \begin{pmatrix} \beta_{0L} + x_{i1}\beta_{1L} \\ \beta_{0K} + x_{i1}\beta_{1K} \\ \beta_{0t} + x_{i1}\beta_{1t} \end{pmatrix}$$

This is efficient in that both sexes can be estimated in one model; therefore all data can be used to estimate other effects that have small associated sample sizes, and we do not have to ponder differences in effects between models for males and models for females.

Also, for the base model with only sex as covariates, the von Bertalanffy parameters estimated from the entire sample will be identical to parameters estimated when model fits are performed separately for each sex (i.e., the estimated parameters for each sex will be the same). This is because both models have six parameters and are able to represent two points in three-dimensional space without constraints. This will be illustrated numerically in the walleye pollock example given later.

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Modeling Pacific ocean perch depth analysis

In Alaska, Pacific ocean perch (POP) are found in the Gulf of Alaska (GOA) and throughout the Aleutian Islands (AI). The data selected for this study were from multispecies Alaska Fisheries Science Center (AFSC) bottom trawl surveys. A preliminary examination of growth data from these regions indicated that there appeared to be little difference in POP von Bertalanffy parameters between these regions. Therefore these data were combined, and it was decided to examine whether von Bertalanffy growth parameters for these regions could be modeled as a function of bottom depth at point of capture, which varied from 68 to 560 m. Generally, because of diet and temperature effects, growth is often thought to slow at greater depths (Thresher et al. 2007). The modeling technique extends that used to model sex difference:

$$\log\begin{pmatrix} L_{\infty,i} \\ K_i \\ t_{0i}+10 \end{pmatrix} = \begin{pmatrix} \beta_{0L}+x_{i1}\beta_{1L}+\log(\text{depth}_i)\beta_{2L} \\ \beta_{0K}+x_{i1}\beta_{1K}+\log(\text{depth}_i)\beta_{2K} \\ \beta_{0t}+x_{i1}\beta_{1t}+\log(\text{depth}_i)\beta_{2t} \end{pmatrix}$$

Modeling sablefish latitudinal analysis

Sablefish along the West Coast of North America have an extremely large latitudinal range occurring from 32.3°N off southern California to 60.6°N in the GOA (measured in decimal degrees). The sablefish surveys and fisheries utilize a mixture of gear types, and so we decided to include both fishery and survey data in this analysis. It is well known that sablefish caught along the US West Coast (WC; which includes Washington, Oregon, and California) grow to a much smaller size than sablefish caught in the GOA (Kimura et al. 1993, 1998). Therefore, the WC and GOA data sets seemed attractive for modeling von Bertalanffy growth parameters as a function of latitude. Sablefish from the AI were considered for this exercise, but preliminary results exhibited a pattern of residuals indicating growth differences could not be explained by latitudinal differences. The model used for sablefish was virtually identical to that used for POP, but with latitude (lat) replacing bottom depth:

$$\log\begin{pmatrix} L_{\infty,i} \\ K_i \\ t_{0i}+10 \end{pmatrix} = \begin{pmatrix} \beta_{0L}+x_{i1}\beta_{1L}+\log(\text{lat}_i)\beta_{2L} \\ \beta_{0K}+x_{i1}\beta_{1K}+\log(\text{lat}_i)\beta_{2K} \\ \beta_{0t}+x_{i1}\beta_{1t}+\log(\text{lat}_i)\beta_{2t} \end{pmatrix}$$

Modeling walleye pollock year-class analysis

Walleye pollock are extremely abundant in the eastern Bering Sea (EBS), supporting annual catches over the past 20 years generally exceeding 1 000 000 tonnes (t)·year^{-1} (Ianelli et al. 2005). The data used in this analysis were collected by the AFSC in annual multispecies bottom trawl surveys. Because of their relatively short lifespan and strong variation in year-class strength, pollock are an ideal species for modeling the variation in von Bertalanffy growth parameters as a function of year class. Generally, it is believed that density-dependent growth effects, such as year-class strength, could affect growth (Quinn and Deriso 1999). It is important that all year classes being modeled contain essentially the full age range from young (1–2 years) to old (at least 12–13 years) fish; otherwise estimates of year-class effects can be biased. To accomplish this, we included year-class effects only for the 1981 to 1993 year classes. Fish in other year classes did not receive a year-class effect or, alternatively, had these effects fixed at zero. The model used for walleye pollock was

$$\log\begin{pmatrix} L_{\infty,i} \\ K_i \\ t_{0i}+10 \end{pmatrix} = \begin{pmatrix} \beta_{0L}+x_{i1}\beta_{1L}+\beta_{2L,y(i)} \\ \beta_{0K}+x_{i1}\beta_{1K}+\beta_{2K,y(i)} \\ \beta_{0t}+x_{i1}\beta_{1t}+\beta_{2t,y(i)} \end{pmatrix}$$

Here, $\beta_{2L,y(i)}$, for example, refers to an effect on $\log(L_\infty)$ due to the year class $y(i)$, which is the year class to which fish i happened to belong. In our example, we model 13 year classes, so 39 parameters are added to this model beyond sex differences. This is equivalent to 39 dummy variables in the full matrix representation. The year-class effects are treated the same as the other fixed effects.

Results from modeling the variation in von Bertalanffy growth parameters due to year classes suggested that year-class strength, in fact, might be influencing these parameters. We therefore regressed pollock von Bertalanffy parameters directly on year-class strength described by the log(number of 1-year-olds). Functionally, this is the same model used to model POP depth and sablefish latitude. Note, however, that this model requires knowing the year class of every specimen.

Fig. 5. Modeled von Bertalanffy growth parameter multipliers, $\exp(x_2\beta_{2t})$, estimated from the sablefish (*Anoplopoma fimbria*) EVB latitude model, that describe the effect that log(latitude), x_2, has on (*a*) L_∞, (*b*) K, and (*c*) t_0.

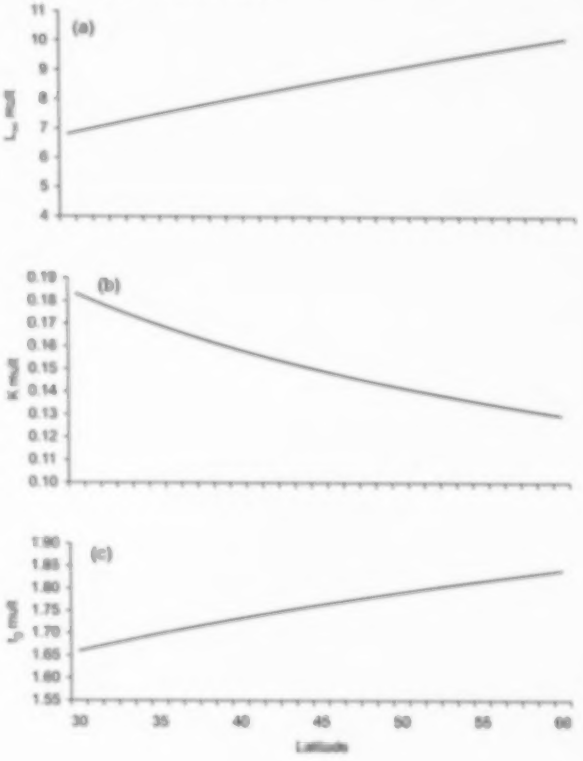

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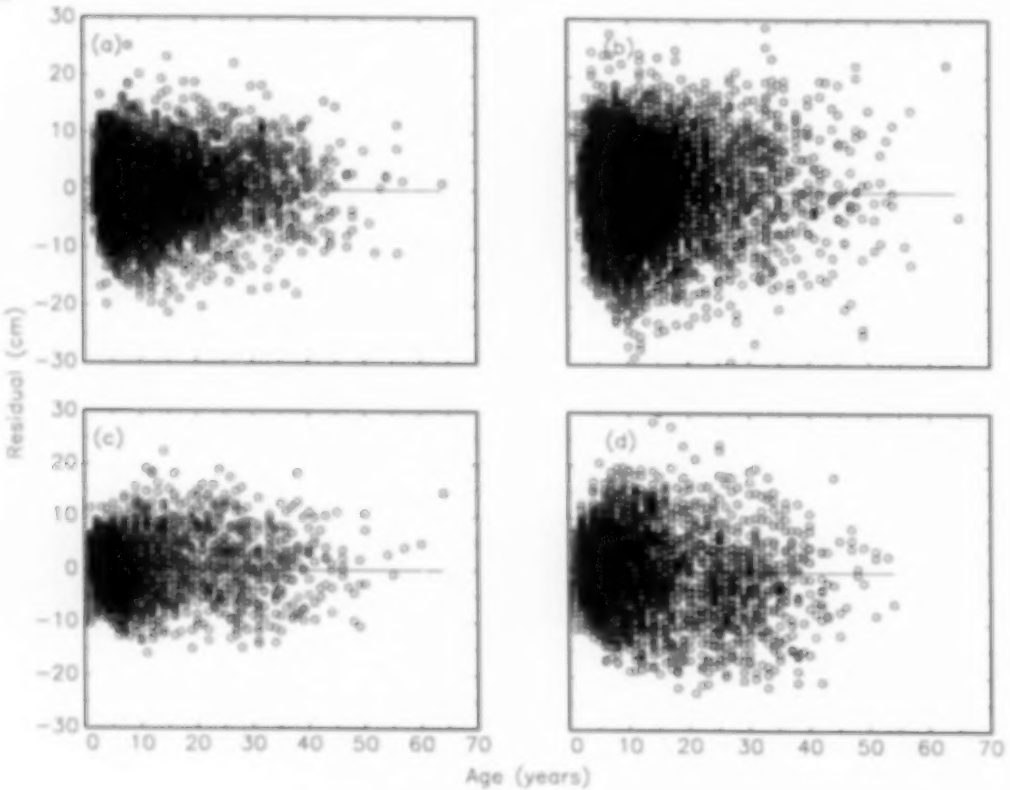
Table 5. Comparison of regional von Bertalanffy parameter estimates for sablefish (*Anoplopoma fimbria*) using the SVB and EVB models.

Estimate	Region	Sex	L_∞	K	t_0	SE(L_∞)	SE(K)	SE(t_0)	SSR
SVB	GOA	Male	68.183	0.267	−2.286	0.111	0.005	0.114	260 610
		Female	81.858	0.191	−2.393	0.190	0.003	0.095	517 105
	WC	Male	59.263	0.271	−2.739	0.172	0.007	0.105	100 958
		Female	66.785	0.275	−2.004	0.200	0.006	0.090	233 139
EVB	GOA	Male	68.109	0.274	−2.048	0.113	0.005	0.092	259 904
		Female	80.784	0.208	−2.021	0.140	0.003	0.067	510 561
	WC	Male	58.400	0.313	−2.364	0.130	0.006	0.087	94 210
		Female	68.557	0.240	−2.359	0.145	0.004	0.078	212 851

Note: SE, standard error; SSR, residual sum of squares. Regions: WC, West Coast; GOA, Gulf of Alaska.

Fig. 6. Residual plots calculated from the sablefish (*Anoplopoma fimbria*) EVB latitude model fits with fish age along the x axis. Data are stratified by region (Aleutian Islands (AI), West Coast (WC)) and sex (males, females): (*a*) AI males, (*b*) AI females, (*c*) WC males, and (*d*) WC females.



Comparing the extended and standard von Bertalanffy models

We refer to the models described in this paper as extended von Bertalanffy models (EVB). Results from fitting the EVB model are different from the standard least squares estimates from a defined region, because EVB estimates can be viewed as being resolved to the individual fish (e.g., resolved to a male specimen captured at depth 52.56 m), whereas the standard model (SVB) calculates von Bertalanffy parameter collectively for a defined region. Therefore, to arrive at regional von Bertalanffy estimates from the EVB model, specimens must be selected from the specific region, the EVB parameter estimates applied to all selected fish from that region, and then the von Bertalanffy parameters averaged. The EVB averages and their standard errors can be compared with the regional SVB estimates and their standard errors. Also, the residual sum of squares for the SVB model can be compared directly with the residuals for the EVB model over the same regional collection.

For example, suppose we wish to compare the EVB modeling results for some sex and region, with depth as a covariate, with the results from the SVB model for the same sex and region. The comparison can then be made as follows. (*i*) Select data for all specimens (n) to be used in the

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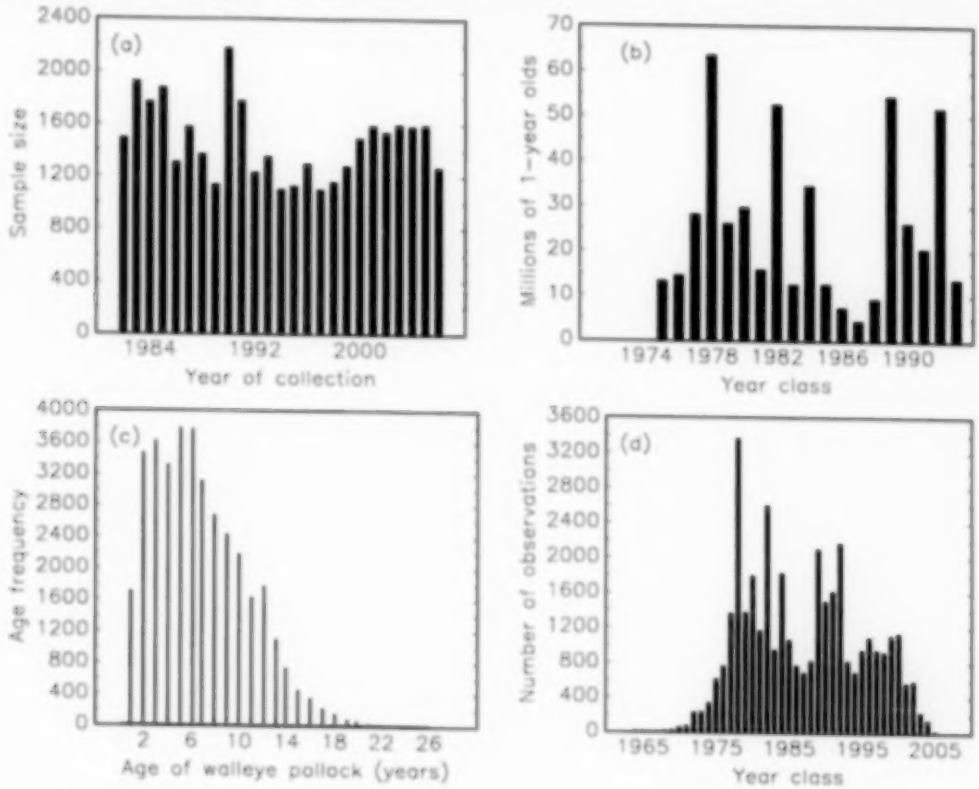
Fig. 7. Histograms for walleye pollock (*Theragra chalcogramma*) age–length data, showing (*a*) year of collection, (*b*) year-class strength (Ianelli et al. 2005), (*c*) specimen ages, and (*d*) year classes.



SVB model fit. Fit the SVB model using nonlinear least squares estimates and the standard error of the parameter estimates on the logarithmic scale in the usual way. (*ii*) Suppose that the EVB has been fit to a broader sample, perhaps over two regions and including both sexes and depth on the logarithmic scale. The estimated parameters are $\hat{o}' = [\hat{\beta}_{0L}, \hat{\beta}_{0K}, \hat{\beta}_{0t}, \hat{\beta}_{sL}, \hat{\beta}_{sK}, \hat{\beta}_{st}, \hat{\beta}_{dL}, \hat{\beta}_{dK}, \hat{\beta}_{dt}]$ with 9×9 covariance matrix estimate $\hat{\Sigma}(\hat{o})$. Consider the vector $x' = \{1, 0, 0, \bar{s}, 0, 0, \bar{d}, 0, 0\}$, where $\bar{s}$ and $\bar{d}$ are averages of the sex and log(depth) variables, based on the n selected observations. Sex ($\bar{s}$) will be 0 or 1 if only a single sex was selected. On the log scale then, $\log(\hat{L}_\infty) = x'\hat{o}$ and $\text{var}(\log(\hat{L}_\infty)) = x'\hat{\Sigma}(\hat{o})x$. It follows that $\hat{L}_\infty = \exp(x'\hat{o})$, and by the delta method (Seber 1973), $\text{var}(\hat{L}_\infty) = \exp(2x'\hat{o})(x'\hat{\Sigma}(\hat{o})x)$. Estimates of $\hat{K}$ and $\hat{t}_0$, and their variances, can be calculated in a similar manner. However, when applying this variance formula, it should be noted that $\log(t_0 + 10)$ is what is actually being estimated on the log scale. (*iii*) The von Bertalanffy parameters and their standard errors for the SVB and EVB methods are now directly comparable. Also of interest is a comparison of the sum of squared residuals for the SVB and EVB estimates, but with the sample for the EVB residuals restricted to the same n observations used in calculating the SVB estimates. The model with the smaller sum of squared residuals over a given region and sex would appear to provide the better regional von Bertalanffy parameter estimates.

Results

Sum of squared residuals (SSR) and the minimum information theoretical criterion (AIC) (Table 1) provide useful measures of goodness of fit for the relevant EVB models (i.e., models fit without sex, with sex, and with sex and covariates). These data show that for the POP, sablefish, and walleye pollock models, fits improved with the addition of further information (i.e., with the addition of sex and covariate information) as measured by decreasing values of SSR and AIC. The SSR values were used to calculate the following F tests, which showed that covariates were significant in all model fits. In addition, the AIC values indicate that including covariates results in improved fits so than none of the models appear overparameterized.

Results for Pacific ocean perch

The POP data analysis was based on 16 182 observations of catches taken from trawl surveys in the AI and GOA from 1986 to 2005 in depths from 68 to 658 m (Fig. 1). Pacific ocean perch are a long-lived species with sampled ages ranging from 1 to 104 years, implying year classes from 1894 to 2004 (Fig. 1). Fitting the EVB model to these data (Table 2) showed that although depth was a statistically sig-

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Table 6. Parameter estimates from fitting the EVB model, with year classes, to walleye pollock (*Theragra chalcogramma*) data from the eastern Bering Sea.

Type	Parameter	Estimate	SE(Est.)	CV(Est.)	*t* value	*P* value
Constant	β_{0L}	4.15143	0.00301	0.00072	1379.34892	0.00001
	β_{0K}	−1.44708	0.01020	−0.00705	−141.80817	0.00001
	β_{0t_0}	2.30068	0.00212	0.00092	1083.88928	0.00001
Sex	β_{1L}	0.08488	0.00355	0.04184	23.89893	0.00001
	β_{1K}	−0.11240	0.01118	−0.09945	−10.05567	0.00001
	β_{1t_0}	−0.00239	0.00251	−1.05301	−0.94966	0.34229
1981 year class	β_{2L}	0.08068	0.01385	0.17172	5.82355	0.00001
	β_{2K}	0.04158	0.00882	0.21210	4.71465	0.00001
	β_{2t_0}	0.09927	0.01303	0.13130	7.61601	0.00001
1982 year class	β_{3L}	0.09112	0.01097	0.12038	8.30707	0.00001
	β_{3K}	0.12493	0.01479	0.11838	8.44767	0.00001
	β_{3t_0}	0.10572	0.01815	0.17169	5.82462	0.00001
1983 year class	β_{4L}	0.05851	0.01528	0.26115	3.82920	0.00013
	β_{4K}	0.06356	0.01444	0.22712	4.40305	0.00001
	β_{4t_0}	0.02065	0.00930	0.45020	2.22123	0.02634
1984 year class	β_{5L}	0.06224	0.01156	0.18574	5.38386	0.00001
	β_{5K}	0.03429	0.01106	0.32250	3.10076	0.00193
	β_{5t_0}	0.06685	0.01303	0.19498	5.12882	0.00001
1985 year class	β_{6L}	0.06010	0.01743	0.28996	3.44880	0.00056
	β_{6K}	−0.48159	0.04224	−0.08771	−11.40150	0.00001
	β_{6t_0}	−0.30016	0.02560	−0.08528	−11.72576	0.00001
1986 year class	β_{7L}	−0.44524	0.03704	−0.08320	−12.01948	0.00001
	β_{7K}	−0.38438	0.02990	−0.07777	−12.85776	0.00001
	β_{7t_0}	−0.46847	0.04333	−0.09249	−10.81164	0.00001
1987 year class	β_{8L}	−0.38296	0.05178	−0.13520	−7.39627	0.00001
	β_{8K}	−0.26178	0.04338	−0.16571	−6.03459	0.00001
	β_{8t_0}	−0.31009	0.04720	−0.15222	−6.56951	0.00001
1988 year class	β_{9L}	−0.16222	0.03326	−0.20501	−4.87789	0.00001
	β_{9K}	−0.32244	0.03859	−0.11969	−8.35474	0.00001
	β_{9t_0}	−0.28738	0.03663	−0.12745	−7.84641	0.00001
1989 year class	β_{10L}	−0.41700	0.03884	−0.09315	−10.73545	0.00001
	β_{10K}	−0.31883	0.05095	−0.15979	−6.25811	0.00001
	β_{10t_0}	−0.12710	0.01225	−0.09635	−10.37909	0.00001
1990 year class	β_{11L}	−0.05304	0.00562	−0.10601	−9.43325	0.00001
	β_{11K}	−0.06441	0.00847	−0.13150	−7.60483	0.00001
	β_{11t_0}	−0.06093	0.00671	−0.11013	−9.08049	0.00001
1991 year class	β_{12L}	−0.10883	0.01204	−0.11062	−9.04016	0.00001
	β_{12K}	−0.05426	0.01342	−0.24725	−4.04454	0.00005
	β_{12t_0}	−0.03385	0.00839	−0.24793	−4.03336	0.00006
1992 year class	β_{13L}	−0.05306	0.01197	−0.22551	−4.43443	0.00001
	β_{13K}	−0.06647	0.00929	−0.13983	−7.15141	0.00001
	β_{13t_0}	−0.08906	0.01121	−0.12591	−7.94195	0.00001
1993 year class	β_{14L}	−0.06939	0.00947	−0.13647	−7.32744	0.00001
	β_{14K}	−0.07723	0.01074	−0.13908	−7.18991	0.00001
	β_{14t_0}	−0.03934	0.00997	−0.25341	−3.94624	0.00008

Note: Degrees of freedom (df) for the *t* value is 36 705. SE(Est.), standard error of the estimate; CV(Est.), coefficient of variation of the estimate.

nificant explanatory variable affecting von Bertalanffy growth parameters ($\bar{F} = 69.1$ with df = 3, 16 173 and $P < 0.00001$), the overall influence of depth multipliers on von Bertalanffy growth parameters was only 6% for L_∞ and K between the extreme range of sampled depths (Fig. 2).

A comparison of SVB and EVB parameter estimates for the AI and GOA regions (Table 3), by sex, indicates that model parameter estimates differed more between regions, as measured by Euclidean distance in parameter space, for SVB estimates than for EVB estimates. Although the residuals from the EVB model plotted against age showed no bias (Fig. 3), the SSR values were larger for the EVB model (which included data from both the AI and GOA and the depth of capture), which seems to indicate that the EVB model fit the regional data a little worse than the SVB model (Table 3). These results suggest that there are factors

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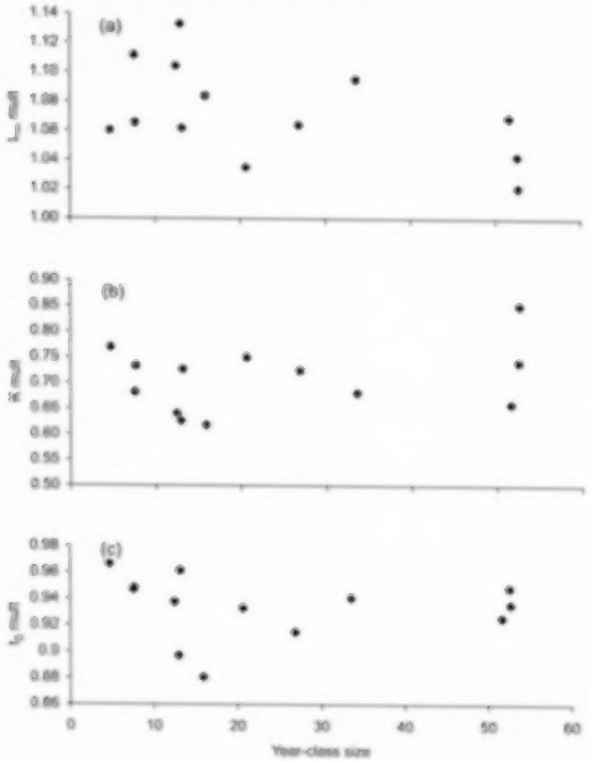
Fig. 8. Modeled von Bertalanffy growth parameter multipliers, $\exp(\beta_{2,y(i)})$, estimated from the walleye pollock (*Theragra chalcogramma*) EVB year-class model, that describe the effect that year class, y(i), has on (*a*) L_∞, (*b*) K, and (*c*) t_0.



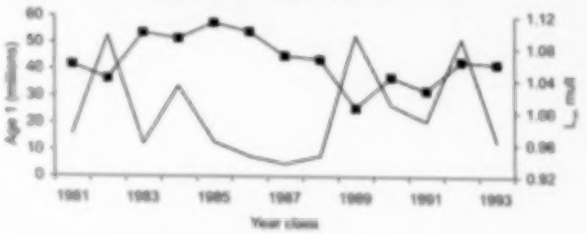
other than depth of capture that affect growth between the two regions or that the linear log-scale model did not adequately capture this relationship.

Sablefish results

The sablefish data analysis was based on 31 870 observations of catches taken from surveys and fisheries along the WC and in the GOA from 1978 to 2005 from 32.4 N to 60.6 N latitude (Fig. 4). Sablefish are a long-lived species with sampled ages ranging from 0 to 65 years, implying year classes from 1922 to 2003 (Fig. 4). Fitting the EVB model to these data (Table 4) showed that latitude was a statistically significant explanatory variable affecting von Bertalanffy growth parameters ($\tilde{F} = 4\,052.7$ with df = 3, 31 861 and $P < 0.00001$). The overall influence of latitude multipliers on sablefish growth parameters L_∞ and K was around 40% between the extreme ranges of sampled latitude (Fig. 5).

A comparison of SVB and EVB parameter estimates for the WC and GOA regions (Table 5), by sex, as measured by Euclidean distance in parameter space indicates that similar regional differences were measured by the two models. Again, the residuals from the EVB model fits plotted against age, for regions and sexes, showed no bias (Fig. 6). Interestingly, the SSR values were smaller for the EVB model (which included data from both the WC and GOA and the latitude of capture), which seems to indicate that the EVB model fit the regional data better than SVB model (Table 5). These results suggest that latitude captured significant factors that affect growth of sablefish between the two regions.

Fig. 9. Plot showing the negative correlation ($\rho = -0.498$) between year-class strength (solid line) in millions of 1-year-olds and L_∞ multipliers (solid squares) for specific year classes.



Walleye pollock results

The walleye pollock data analysis was based on 36 750 observations of catches taken from bottom trawl surveys in the EBS from 1982 to 2006 (Fig. 7). Walleye pollock ranged in ages from 0 to 26 years, implying year classes from 1964 to 2005 (Fig. 7). Plotting the strength of these year classes, estimated from stock assessment models as 1-year-olds (Ianelli et al. 2005), show that year-class strength over these years varied by a factor of 14. Fitting the EVB model to these data (Table 6) showed that year class (1981–1993) was a statistically significant explanatory variable affecting von Bertalanffy growth parameters ($\tilde{F} = 59.0$ with df = 39, 36 705 and $P < 0.00001$). The overall range of influence of year class on walleye pollock growth parameter multipliers (Fig. 8) was around 11% for L_∞ and 40% for K.

The correlation of year-class strength with year-class multipliers for L_∞ (–0.498), K (+0.308), and t_0 (–0.064) were consistent with larger year classes growing to smaller maximum sizes. However, only the correlation with the L_∞ multipliers was significant at the $\alpha = 0.05$ level using a one-tailed t test ($P < 0.04$, df = 13). Year-class strength is plotted against L_∞ multipliers (Fig. 9).

To further examine the possible influence of year-class strength on walleye pollock von Bertalanffy parameters, von Bertalanffy parameters were regressed directly on log(number of 1-year-olds) (Table 1, bottom model). The interesting result from this model fit was that the regression coefficients for L_∞ and K were both significantly different from zero ($P < 0.00001$).

A comparison of SVB and EVB parameter estimates was made for walleye pollock in the EBS. In this comparison, under the SVB model, males and females were fit by separating the data and then estimating parameters in the usual way. For the EVB model, parameters were fit assuming that sex was the only covariate. In this comparison, all von Bertalanffy parameter estimates, standard errors, and SSR values were identical for the two methods of estimation (Table 7).

Discussion

Others have used the von Bertalanffy growth model to examine the effects of geography and environmental factors

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Table 7. Comparison of von Bertalanffy parameter estimates for walleye pollock (*Theragra chalcogramma*) from the eastern Bering Sea using the SVB and EVB (using only sex as a covariate) models.

Estimate	Sex	L_∞	K	t_0	SE(L_∞)	SE(K)	SE(t_0)	SSR
SVB	Male	64.724	0.206	−0.287	0.170	0.002	0.019	443 200
	Female	70.497	0.184	−0.311	0.197	0.002	0.020	597 434
EVB	Male	64.724	0.206	−0.287	0.179	0.002	0.020	
	Female	70.497	0.184	−0.311	0.179	0.002	0.020	

Note: The sum of squared residuals (SSR) for the EVB model over the entire data set was 1 040 633, which is the same as the SSR summed for the two SVB models. SE, standard error.

on growth. For example, Braaten and Guy (2002) regressed von Bertalanffy parameter estimates on latitude for five species of fish found along the Missouri River. Helser and Lai (2004) used a Bayesian hierarchical growth model to model latitudinal effect on the growth of largemouth bass (*Micropterus salmoides*), whereas Dorn (1992) modified the von Bertalanffy growth model to estimate the effects of environmental factors on the growth of Pacific whiting (*Merluccius productus*). However, there appears to be remarkably little written concerning the simple extension to the von Bertalanffy growth model described here.

This paper illustrates that the von Bertalanffy growth model can be extended easily to include explanatory variables that model variations in growth parameters. A useful conceptual analogy is that the explanatory variables make adjustments to average von Bertalanffy growth parameters. Another quite different analogy is that explanatory variables partition the population into subsets, which have their own von Bertalanffy parameters. Results from the walleye pollock analysis show the usefulness of the partition paradigm because the EVB model that includes only sex as an explanatory variable gives the same results as partitioning the data into male and female data sets and estimating the parameters separately.

For sablefish, the EVB model results show that L_∞ for sablefish increases dramatically with latitude. The fact that K decreases at greater latitude agree with the common finding that L_∞ and K are statistically (Kimura 1980; James 1991) and biologically (Gunderson and Dygert 1988; Helser and Lai 2004) negatively correlated. For sablefish, the SSR calculated from the EVB model for the GOA and WC regions for males and females separately were smaller than those for the SVB model, which suggests that latitude was a better predictor of length-at-age than sampling region. In this case, the differences in parameter estimates between regions were large for both the SVB and EVB models, while the differences in parameter estimates between the SVB and EVB models were small within both regions.

In interpreting results from the EVB model, it is important to distinguish between explanatory variables present in the model and the causal mechanisms behind these variables. For example, in the case of POP, it is generally believed that females undergo a winter migration to greater depths for the purpose of releasing larvae (Love et al. 2002). However, because sex is included in the growth model, this hopefully would not be a factor. Although it may be simply that those fish preferring to reside at greater depths grow on average to a smaller maximum size, thereby accounting for the estimated negative effect of depth on maximum size, there remains the possibility that sex and depth effects are being confounded by sampling effects. For sablefish, the possible factors contributing to observed growth are also complex. Because fishing and survey gear differ between the GOA and the WC, with longlines predominant in the GOA and trawl and pot gear more important off the WC (Kimura et al. 1998), this suggests that gear selectivity may affect modeling results. The fact that sablefish are known to undergo long-distance, age-related migrations (Heifetz and Fujioka 1991; Kimura et al. 1998) also makes the simple model based on latitude seem a little murky. However, it is also remarkable that the EVB model, which includes latitude but not region, outperformed the regional von Bertalanffy growth estimates in terms of having smaller SSRs.

For walleye pollock, we wanted to make sure that year-class effects were only estimated for those year classes that included a fairly complete range of ages. This meant that only the 1981 to 1993 year classes could be included. Unfortunately, this excluded the 1978 year class, which was the strongest of any reported pollock year class and therefore lessened our ability to detect a significant relationship between year-class strength and von Bertalanffy growth parameters. Nevertheless, the correlation between L_∞ estimates and year-class strength as measured by the number of 1-year-olds was $\rho = -0.498$, which was significant at $\alpha = 0.05$ for the one-tailed t test. The correlation between L_∞ and K for these year classes was $\rho = -0.830$, which was significant at $\alpha = 0.001$ for the two-tailed t test. The walleye pollock model, which included the number of 1-year-olds as a measure of year-class strength, gave results indicating that the L_∞ and K were both significantly influenced by year-class strength ($P < 0.00001$). This supports the general observation that a model focused on a narrow relationship will often have the better chance of obtaining statistically significant results.

It seems clear that the EVB models are a straightforward extension of the usual SVB model. The sablefish example, which compared the EVB and SVB base models with sex only, indicates that up to this level of analysis, the EVB and SVB models are identical for practical purposes. This suggests that when desired, the strategy of calculating averages of EVB parameters and estimating standard errors was not unreasonable.

It appears that the EVB model can be used to relate von Bertalanffy growth parameters to a variety of geographic and environmental factors. In fact, the methods used in this paper appear to be generally applicable to other nonlinear models besides the von Bertalanffy growth curve. However,

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care must be taken to assure that the data support the modeling being attempted. Model fits and results appear to flow easily from standard nonlinear least square methods. The more difficult problem, true with most models, is to properly interpret the modeling results.

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Species traits influence the genetic consequences of river fragmentation on two co-occurring redhorse (*Moxostoma*) species

Scott M. Reid, Chris C. Wilson, Leon M. Carl, and Troy G. Zorn

Abstract: We used microsatellite DNA markers to test whether fragmentation of the Trent River (Ontario, Canada) has reduced genetic diversity and increased genetic differentiation among populations of river redhorse (*Moxostoma carinatum*) and shorthead redhorse (*Moxostoma macrolepidotum*). Allelic richness of both species was significantly greater along the free-flowing Muskegon River (Michigan, USA) than along the fragmented Trent River. Contrary to expectations, there was no evidence of a fragment length effect on genetic diversity, recent population bottlenecks, or increased relatedness among individuals in fragmented populations. High levels of linkage disequilibrium indicate extinction–recolonization population dynamics along the Trent River. For both species, pairwise F_{ST} tests identified weak but statistically significant population differentiation. In the Trent River, differentiation was significantly greater for river redhorse than for shorthead redhorse and, for both species, greater than in the Muskegon River. Moderate fragmentation effects likely reflect the permeability of the dam-lock system to redhorse movement. Differences between species indicate that as a result of smaller effective population sizes, habitat specialists and species at the periphery of their geographic range are more sensitive to river fragmentation.

Résumé : Des marqueurs microsatellites de l'ADN nous ont servi à tester si la fragmentation de la rivière Trent (Ontario, Canada) a réduit la diversité génétique et augmenté la différentiation génétique chez les populations de suceurs ballots (*Moxostoma carinatum*) et de suceurs rouges (*Moxostoma macrolepidotum*). La richesse allélique des deux espèces est significativement plus élevée dans le cours de la rivière Muskegon (Michigan, É.-U.) à écoulement libre que dans le cours fragmenté de la Trent. Contrairement à nos attentes, il n'y a aucune indication d'effet de la longueur d'un fragment sur la diversité génétique, ni de goulots d'étranglement récents dans la population, ni d'une parenté accrue entre les individus dans les populations fragmentées. De forts niveaux de déséquilibre de liaison indiquent l'existence d'une dynamique de population de type extinction–recolonisation le long de la Trent. Chez les deux espèces, les tests appariés F_{ST} identifient une différenciation des populations faible, mais statistiquement significative. Dans la Trent, la différenciation est significativement plus importante chez le suceur ballot que chez le suceur rouge et elle est plus forte, pour les deux espèces, que dans la Muskegon. Ces effets modérés de la fragmentation sont vraisemblablement le reflet de la perméabilité du système de barrages et d'écluses aux déplacements des suceurs rouges. Les différences entre les espèces indiquent que, comme résultat de leur taille de population réduite, les spécialistes de l'habitat et les espèces à la périphérie de leur aire géographique de répartition sont plus sensibles à la fragmentation des rivières.

[Traduit par la Rédaction]

Introduction

Hydrological and ecological changes associated with dams have contributed to the loss or reduction of migratory anadromous fish populations, smaller-bodied riverine fish species and invertebrates, and taxa dependent on flooding (Pringle et al. 2000). As a result of changes to population size and gene flow, dams can reduce genetic diversity within isolated fish populations and increase genetic differentiation among fish populations (Neraas and Spruell 2001; Yamamoto et al. 2004). In isolated populations, low genetic diversity can result from genetic drift, inbreeding, bottlenecks, and founder effects. At larger spatial scales, by restricting the movements of individuals, dams can increase genetic differentiation between previously connected or panmictic fish populations (Meldgaard et al. 2003), create upstream–downstream gradients in genetic diversity (Yamamoto et al. 2004), and disrupt the regional equilibrium between drift and immigration of new alleles in populations (Hutchison and Templeton 1999).

To date, research on the effects of riverine fragmentation on genetic diversity and population structure of fishes has been limited to single-species studies. Multispecies comparisons are needed to identify the common effect of landscape-level factors on genetic structure (Bermingham and Moritz

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1998; Castric and Bernatchez 2004) and to clarify the influence of species traits on the sensitivity of riverine fishes to landscape-level changes. The responses of aquatic and terrestrial organisms to habitat fragmentation are variable, often reflecting differences in species traits (Debinski and Holt 2000; Srikwan and Woodruff 2000; Cushman 2006). Generally, habitat specialists and (or) rare species are more sensitive to decreasing patch size and increasing isolation than habitat generalists and (or) common species (Ewers and Didham 2006). It is expected that genetic consequences of fragmentation will be influenced by ecological, demographic, and life-history characteristics that affect gene flow and subsequent population subdivision and genetic drift (Lesica and Allendorf 1995; Vucetich and Waite 2003; Zayed et al. 2005). For riverine fishes, among-species differences in population subdivision have been attributed to differences in spawning ecology, dispersal potential, and effective population size (Castric and Bernatchez 2004; Whiteley et al. 2004).

In this study, the genetic consequences of river fragmentation by dams on two redhorse species (river redhorse (*Moxostoma carinatum*) and shorthead redhorse (*Moxostoma macrolepidotum*)) were compared. Redhorse species (genus *Moxostoma*) are relatively large, laterally compressed, and superficially similar suckers (family Catostomidae) that are typically found in larger streams and rivers, but also in impoundments and lakes (Jenkins and Burkhead 1993; Scott and Crossman 1998). Redhorse species are good model species for investigating fragmentation effects as (*i*) they undertake seasonal migrations to spawning and overwintering habitats (Hackney et al. 1968; Grabowski and Isely 2006) and are therefore sensitive to barriers to movement, (*ii*) they have been reported to be sensitive to habitat changes related to dams (Quinn and Kwak 2003), (*iii*) growth, abundance, and reproductive characteristics of other sucker species have been correlated to habitat quantity, quality, and isolation (Trippel and Harvey 1987; Chen and Harvey 1999), (*iv*) species-level differences in regional distribution, abundance, life-history characteristics, and habitat preferences permit comparisons of sensitivity to habitat fragmentation, and (*v*) unlike sport fishes, the effects of dams will not be obscured by past stocking or high rates of fishing mortality.

The two redhorse species investigated in this study differ in their proximity to the core of their species range, habitat specialization, and population characteristics. Compared with shorthead redhorse, river redhorse has a small, discontinuous geographic range (Scott and Crossman 1998; NatureServe 2005), is near the northern edge of its geographic range in the Trent River (Scott and Crossman 1998), has a stronger association with free-flowing riverine habitats (Yoder and Beaumier 1986), and matures at later age (Reid 2006). In Canada, river redhorse is a species of special concern (Committee on the Status of Endangered Wildlife in Canada (COSEWIC) 2005) and is considered imperilled in neighbouring Great Lakes states (NatureServe 2005). These differences are expected to translate into different effective population sizes (Lesica and Allendorf 1995; Frankham 1996; Zayed et al. 2005) and, correspondingly, different sensitivities to fragmentation effects on gene flow.

Genetic diversity and population structure of river redhorse and shorthead redhorse in two Laurentian Great Lakes basin rivers with contrasting levels of fragmentation were characterized using microsatellite DNA. It was hypothesized that river fragmentation would increase population subdivision and reduce genetic diversity and that fragmentation effects would be more pronounced for river redhorse than for shorthead redhorse. The effect of fragmentation was evaluated by testing for evidence of (*i*) reduced genetic diversity and recent bottlenecks within fragmented populations, (*ii*) increased population subdivision, and (*iii*) an additive effect of dams on population differentiation. Demographic and mark–recapture data collected as part of a parallel study (Reid 2007) indicate that source–sink population dynamics (sensu Harrison 1991) operate along the Trent River. Spawning runs were absent from the smallest river fragments, and mark–recapture data indicate that a small percentage of individuals move between fragments, either upstream through the navigational locks or downstream over the dams (Reid 2007). Therefore, the persistence of small fragment populations is likely dependent on migrants from larger fragments. Individual assignment tests and a genetic-based framework (Tero et al. (2003) developed to evaluate models of movement along linearly arranged populations were applied to evaluate whether genetic data provide evidence of source–sink dynamics along the Trent River.

Materials and methods

Sample collection

Between 2001 and 2004, redhorse species were sampled from the Trent River, Ontario, and Muskegon River, Michigan, using a 5 kW pulsed DC boat-mounted electrofishing unit (Fig. 1). As part of the Trent–Severn Waterway, the Trent River has been highly fragmented by navigational and run-of-the-river hydroelectric dams. Ten river fragments were sampled along a 56 km section of the Trent River between the Hagues Reach Hydroelectric Generating Station and the Bay of Quinte, Lake Ontario. Dams and locks along this reach of the Trent River were constructed during 1838 to 1839 and 1911 to 1913 (Angus 1998). Both species have not been captured upstream of the study reach. For comparison, eight sites were sampled along a 76 km free-flowing reach of the Muskegon River between the Croton Hydroelectric Dam (constructed in 1905) and Muskegon Lake. In contrast to the Trent River, the Muskegon River, a Lake Michigan tributary, has few natural or constructed barriers along its mainstem.

The likelihood of redhorse capture was maximized by targeting shallow, fast-flowing habitats with coarse bed material (gravel, cobble, and boulder) and run or pool habitats immediately downstream (Yoder and Beaumier 1986). Along the Trent River, these habitats were located in tailwater areas downstream of dams. Sampling site selection along the Muskegon River was based on the location of large riffle areas and on boat access. Fin clips were taken and stored either in 95% ethanol or as dried tissue in scale sample envelopes. Redhorses sampled were adult-sized (shorthead redhorse, 40–62 cm total length; river redhorse, 50–80 cm total length) and represented multiple age classes.

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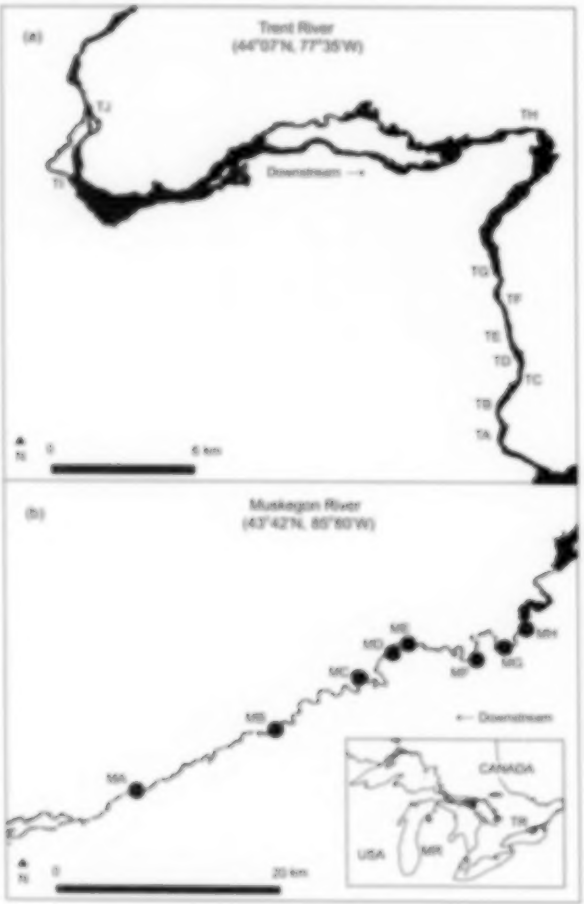
Fig. 1. Locations of redhorse sampling sites along (*a*) the Trent River (Ontario) and (*b*) the Muskegon River (Michigan). River locations within the Laurentian Great Lakes basin are identified in the inset map (TR, Trent River; MR, Muskegon River).



Laboratory methods

DNA was extracted from air-dried and 95% ethanol-preserved fin clips. Tissue samples were placed in a 96-deep-well plate and lysed with 400 µL of lysis buffer (50 mmol·L^{-1} Tris ph 8, 100 mmol·L^{-1} NaCl, 1 mmol·L^{-1} EDTA, 1% SDS *w/v*) with 1.5 µL Proteinase K (20 mg·mL^{-1}). To precipitate the DNA, 16 µL of 5 mol·L^{-1} NaCl and 800 µL of 80% isopropanol were added to each well. Samples were then centrifuged for 45 min at 6200 rpm to pellet the DNA. Supernatant was removed and the pellet was washed with 1000 µL of 70% ethanol to remove excess salts. Plates were vortexed and recentrifuged for 45 min at 6200 rpm; ethanol was carefully removed and plates were left to dry until all ethanol had evaporated. DNA was resuspended in 100–200 µL of 1× TE (10 mmol·L^{-1} Tris, 1 mmol·L^{-1}EDTA). DNA yield and quality was visually assessed by horizontal electrophoreses on a 1.5% agarose gel alongside molecular mass ladders.

Eleven microsatellite DNA loci were amplified using the polymerase chain reaction (PCR) (primer sequences, allele size ranges provided in Supplemental Table S1.[2] Microsatellite primers used were initially developed for Lost River sucker (*Deltistes luxatus*) (Tranah et al. 2001), copper redhorse (*Moxostoma hubbsi*) (Lippe et al. 2004), and robust redhorse (*Moxostoma robustum*) (I. Wirgin, New York University Medical Center, Nelson Institute of Environmental Medicine, Tuxedo, NY 10987, USA, unpublished primers). Over 120 potential polymorphic dinucleotide and tetranucleotide primers have been identified for these three catostomid species. Based on the reported levels of heterozygosity and allele number, a subset of 28 microsatellite primers was evaluated. Suitability was based on the level of polymorphism among individuals and whether primers would reliably amplify. For each primer, four to five samples of each species were amplified. Test samples for both species were collected from the Grand River (Lake Erie basin), Muskegon River, and Trent River. The potential for cross reactivity (i.e., primer–dimer formation) of individual primer pairs was evaluated using AutoDimer (Vallone and Butler 2004). In contrast to Lippe et al. (2004), *Mohu-lav*203, *Mohu-lav*212, and *Mohu-lav*213 were not polymorphic for river redhorse and shorthead redhorse. Lost River sucker (*dlu*) and robust redhorse (RR) loci that were monomorphic, or poorly amplified, included *dlu*434, *dlu*467, *dlu*4139, *dlu*4235, *dlu*4276, *dlu*4300, *dlu*4314, *dlu*4315, RR15, RR24, RR33, RR37, and RR44.

Loci were co-amplified in duplex and triplex reactions (simultaneous amplification of two or three loci in one reaction). For their subsequent detection, each microsatellite locus was amplified using a fluorescent-dye-labelled primer along with an unlabelled primer (Table 1). Polymerase chain reactions were performed in 11 µL total volumes containing 1.5 µL of DNA template, 1.1 µL PCR buffer, 0.8 µL of $MgCl_2$ (25 mmol·L^{-1}), 0.24 µL of dNTPs (10 µmol·L^{-1}), 0.13 µL of *Taq* I DNA polymerase (5U·µL^{-1}), microsatellite primers (10 µmol·L^{-1}) (volumes listed below), and 5.6–6.0 µL of ddH_2O (depending on primer volumes within each multiplex). In the duplex reaction (MULTI_1), primer volumes were 0.05 µL RR13 (FAM) and 0.1 µL RR55 (NED). In the first triplex (MULTI_2), primer volumes were 0.16 µL RR38 (HEX), 0.13 µL *dlu*4184 (NED), and 0.16 µL *dlu*4296 (FAM). Primer volumes in the second triplex (MULTI_3) were 0.1 µL *Mohu-lav* 198 (NED), 0.1 µL *Mohu-lav* 296 (FAM), and 0.2 µL *Mohu-lav* 305 (HEX). Primer volumes in the third triplex (MULTI_4) were 0.10 µL *dlu*45 (FAM), 0.21 µL *dlu*405 (HEX), and 0.10 µL *Mohu-lav*194 (NED). Reactions were amplified in a thermocycler (model PTC-100; MJ Research, Inc., Waltham, Mass.) using an initial denaturation at 94 °C (11 min), followed by 35 cycles of 94 °C (1 min), 55 °C (MULTI_1 and MULTI_2) or 60 °C (MULTI_3 and MULTI_4) (1 min), and 72 °C (1 min), with a final extension at 60 °C (45 min).

[2] Supplementary data for this article are available on the journal Web site (http://cjfas.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 3794. For more information on obtaining material, refer to http://cisti-icist.nrc-cnrc.gc.ca/cms/unpub_e.html., available online from NRC Data Depository).

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Table 1. Site details and associated measures of abundance and genetic diversity for river redhorse (*Moxostoma carinatum*) and shorthead redhorse (*Moxostoma macrolepidotum*) sampled from the Trent River, Ontario.

			M. carinatum				*M. macrolepidotum*			
Site	rkm[a]	Fragment length (km)	*n*	Maximum spring CPUE[b]	A_R	H_O	*n*	Maximum spring CPUE[b]	A_R	H_O
TA	3	3.1	41	39.3	4.40	0.74	48	31.7	8.73	0.78
TB	4.1	1.1	9	1.7	4.36	0.77	43	7.7	8.67	0.78
TC	6.6	2.5	47	15.0	4.25	0.71	51	27.3	8.78	0.74
TD	7.5	0.9	12	4.5	4.02	0.73	21	9.6	8.26	0.73
TE	8.8	1.3	4	1.3	4.09	0.61	11	1.7	8.52	0.69
TF	11	2.2	47	5.7	4.32	0.70	54	18.3	8.59	0.74
TG	13.4	2.4	15	3.0	4.21	0.79	57	9.7	8.86	0.77
TH	23.6	10.2	48	41.3	4.21	0.71	53	37.0	8.30	0.79
TI	46.6	23.0	56	11.3	4.17	0.71	55	23.7	8.91	0.80
TJ	48.9	2.3	35	4.0	4.00	0.71	30	5.7	7.86	0.68
All			314		4.40	0.72	423		8.97	0.76

Note: See Fig. 1 for site locations. CPUE, catch per unit effort; A_R, standardized allelic richness; H_O, observed heterozygosity.

[a]River kilometres (rkm) is the distance in kilometres upstream from river mouth.

[b]Number of individuals per 1000 seconds of boat electrofishing.

After amplification, PCR products were diluted in 11 μL of sterile deionized water and then combined with an internal lane standard composed of formamide, loading buffer, and ROX 350 size standard (Applied Biosystems Inc., Foster City, Calif.). Diluted PCR products were denatured at 96 °C for 2 min and then loaded into a 5% Long Ranger acrylamide gel and electrophoresed on an ABIPrism 377 DNA sequencer. Reactions were visualized using GeneScan software (Applied Biosystems Inc.), and bands were scored by comparison with standard ROX 350 ladder using GenoTyper (Applied Biosystems Inc.) and visual proofreading. Genotypes were checked for scoring errors that might be attributable to stutter-products, large allele dropout, or the presence of null alleles using MICROCHECKER (version 2.2; van Oosterhout et al. 2004).

Data analysis

Patterns of allelic diversity and disequilibrium

The number of alleles (N_A), standardized allelic richness (A_R), observed heterozygosity (H_O) statistics, and allele frequencies were compiled using FSTAT (version 2.9.3; Goudet 2001) and the Microsoft Excel Microsatellite Toolkit (Park 2001). Differences in A_R among sites and among loci were each tested using one-way analysis of variance (ANOVA). Conformation of A_R data to the assumption of normality was assessed with the Shapiro–Wilk test. Analysis of molecular variance (AMOVA) was completed using GenAlEx 6 (Peakall and Smouse 2006). Genotypes at each locus for each population were tested for conformance to Hardy–Weinberg equilibrium (HWE) using GENEPOP (version 3.4; Raymond and Rousset 1995). Fisher's exact test of linkage disequilibrium was performed between all pairs of loci with 10 000 dememorizations, 10 000 batches, and 10 000 iterations per batch. To address the risk of inflated type I errors resulting from multiple tests, significance levels ($p < 0.05$) were adjusted using the Bonferroni correction (Rice 1989).

The paired-sample *t* test was used to test the hypothesis that genetic diversity (A_R and H_O) of the more abundant shorthead redhorse was greater than that of the river redhorse (Zayed et al. 2005). For river redhorse, *dlu*405 (both rivers) and *Mohu-lav*198 (Muskegon River only) did not amplify consistently and (or) were monomorphic. Therefore, the number of loci available for analysis was not consistent across species and rivers. All tests comparing genetic diversity and population differentiation between species and rivers were standardized to the same number of microsatellite loci using FSTAT.

In the Trent River, river fragment length and redhorse abundance are positively correlated (Reid 2007). Populations in short river fragments were therefore hypothesized to have comparatively low levels of genetic diversity. To test for a river fragment size effect on genetic diversity, Spearman's rank correlations (r_S) were calculated between genetic diversity measures (A_R and H_O) and (*i*) river fragment length and (*ii*) maximum spring catch-per-unit-effort (CPUE, an indicator of the number of spawners). By facilitating downstream dispersal and limiting upstream dispersal, the unidirectional downstream flow of water has been hypothesized to create upstream–downstream gradients of genetic diversity (Hernandez-Martich and Smith 1997). Correlations between genetic diversity measures and distance upstream from river mouth were therefore also calculated for both rivers.

The relationship between river fragment length and genetic diversity (A_R and H_O) was also tested by comparing populations grouped into three length classes: small (0.9–1.3 km; $n = 3$); medium (2.2–2.4 km; $n = 4$); and large (>3.1 km; $n = 3$). Fragment length classes differ in the amount of available shallow tailwater habitat (small, ~50–100 m; medium, ~500–700 m; large, >1.0 km) and the demographic characteristics of populations (e.g., number and sex ratio of spring spawners) (Reid 2007). Differences between river fragment length classes were tested with randomization tests (1000 permutations) as implemented in FSTAT. Randomization tests were also used to compare the genetic diversity (A_R and H_O) of redhorse populations in the fragmented Trent River to Muskegon River populations.

By creating small populations that are isolated from im-

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migration and preferred spawning habitats, river fragmentation could trigger population bottlenecks and result in low genetic diversity through either genetic drift or inbreeding (Frankham et al. 2002). Redhorse populations within Trent River fragments were tested for evidence of recent population bottlenecks and inbreeding. Recently bottlenecked populations may exhibit gametic disequilibrium (Waples 2002), reduced genetic diversity (particularly the loss of rare alleles) (Allendorf 1986), and increased heterozygosity relative to that expected at mutation–drift equilibrium (Cornuet and Luikart 1996). Evidence of recent and pronounced reductions in population size was tested using BOTTLENECK (version 1.2.02; Piry et al. 1999) and by calculating Garza and Williamson's (2001) M statistic. When a population undergoes a reduction in its effective population size, allelic diversity is reduced more rapidly than heterozygosity; as a consequence, there is a transient deficiency in the number of alleles (Cornuet and Luikart 1996). BOTTLENECK compares a population's heterozygote excess to that expected to be found at mutation–drift equilibrium. As microsatellite evolution is more similar to the stepwise mutation model (SMM) than the infinite allele model (IAM), a two-phase mutation model with 95% SMM, 5% IAM, and 12% variance of multiple-step mutations was assumed. Simulation iterations (5000) were conducted for each population (Cornuet and Luikart 1996; Piry et al. 1999). Simulations were limited to sites with at least 20 individuals sampled (Luikart and Cornuet 1998). Significance of heterozygote excess over all loci was tested with the Wilcoxon's signed-rank test. Garza and Williamson's (2001) M is the mean of the ratio of the total number of alleles (k) and the number of repeats over the allele size range (r) for each locus. The ratio is based on the expectation that when the effective size of a population is reduced and drift occurs, reductions in allele size range will occur more slowly than the loss of individual alleles. Based on simulations and data from natural populations, values of $M < 0.68$ are indicative of populations that have undergone a recent bottleneck (Garza and Williamson 2001).

To determine globally whether individual redhorse collected from each site were more related than expected under random mating, a Monte Carlo resampling test (IDENTIX; Belkhir et al. 2002) that uses a multilocus estimator ($r_{x,y}$) for pairwise comparisons (Queller and Goodnight 1989) was applied. High relatedness values and (or) excess representation by a few families could be indicative of inbred individuals in a population (Lippe et al. 2006). Tests of both the mean and variance of relatedness coefficients were undertaken, as significantly higher variance can indicate that several independent groups of related individuals were sampled. As several populations did not conform to Hardy–Weinberg expectations, resampling (1000 permutations) was carried out at the genotype level.

Population structure

Differentiation among populations was evaluated using both population-level (F_{ST}) and individual assignment methods. Global F_{ST} and pairwise F_{ST} were estimated using Weir and Cockerham's θ (Weir and Cockerham 1984). F_{ST} values and significance of estimates were calculated with FSTAT. F_{ST} was used instead of R_{ST}, as F_{ST} estimates are more conservative when relatively few (<20) microsatellite loci are used and when populations have recently diverged (Gaggiotti et al. 1999). Tests for population differentiation were limited to sites with at least 20 genotyped individuals.

Genetic distances among population pairs were estimated by computing Cavalli-Sforza and Edwards (1967) genetic chord distances (D_{CE}) in POPULATIONS (version 1.2.28; Oliver Langella, unpublished (1999), http://bioinformatics.org/~tryphon/populations/). D_{CE} was used because it is commonly applied in studies of fish population structure, does not assume any mutation model, and performs well in simulations with microsatellite data (Takezaki and Nei 1996). To visualize the genetic relationships among sites, D_{CE} chord distances were used to build an unrooted neighbour-joining tree in TREEVIEW (version 1.66; Page 1996). Robustness of the typology was evaluated by 1000 bootstrap resamplings as implemented in POPULATIONS.

The effect of dams on genetic differentiation was evaluated by testing for significant correlations between matrices of pairwise genetic distance (F_{ST} and D_{CE} values), geographic distance, and number of dams separating population pairs. As geographic distances between population pairs were greater than habitat width, F_{ST} values were adjusted with the following transformation: $F_{ST}/(1 - F_{ST})$ (Rousset 1997). Significance of correlations was based on Mantel and partial Mantel tests (10 000 permutations) calculated using the software IBD (Bohonak 2002). Using pairwise F_{ST} and D_{CE} estimates from the same set of populations, the paired-sample t test was used to test the hypothesis that genetic differentiation between river redhorse population pairs was greater than for shorthead redhorse populations.

Two approaches were applied to evaluate whether fragmented Trent River populations were in regional equilibrium (i.e., a balance between the loss of alleles due to drift and their replacement by gene flow) or whether genetic drift was more influential than gene flow. Assuming a stepping-stone model of regional population structure, Hutchison and Templeton (1999) interpreted populations of a region to be at equilibrium (CASE I) if (*i*) there is a significant relationship between pairwise F_{ST} genetic and geographic distances separating populations and (*ii*) a scatterplot of pairwise F_{ST} and geographic distances reveals a positive and monotonic relationship over all distance values of a region. The second approach, using a Markov Chain Monte Carlo (MCMC) approach implemented in 2mod (Ciofi et al. 1999; software available from http://www.rubic.rdg.ac.uk/~mab/software.html), calculates the relative likelihood of two alternate models of demographic history: a model of immigration–drift equilibrium versus a model of drift (without equilibrium). The MCMC search was carried out twice for 10^5 iterations with the initial 30 000 discarded as burn-in.

Tero et al. (2003) presented a genetic-based framework to evaluate five hypothetical models of migration along linearly arranged populations. The five models include (*i*) a genetically uniform population model with free gene flow between populations, (*ii*) a fragmented population model without gene flow, (*iii*) a stepping-stone population model, (*iv*) a source-sink model, and (*v*) the classic metapopulation model. The applicability of the different models to given sets of populations is evaluated based on gene flow, population differences in genetic diversity, mutation–drift equili-

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brium, and extinction–replacement dynamics. Characteristics that would support a source–sink population model for the Trent River include gene flow from source to sink populations, greater genetic diversity in source populations relative to sink populations, and high levels of linkage disequilibrium within populations and for the total population set (Tero et al. 2003).

Individual assignment tests of multilocus genotypes were conducted to assign probable source populations as origins of individual redhorse sampled from hypothesized sink populations. Assignment tests were also done to evaluate membership within source populations. Individuals were assigned to a population based on log-likelihood probabilities of their genotypes occurring by chance in potential source populations using GeneClass (version 2; Cornuet et al. 1999; Piry et al. 2004). The Bayesian leave-out method (i.e., remove an individual's genotype from the data set before calculating its log-likelihood probability of assignment to population group) was used for self-assignments of individuals to populations (Rannala and Mountain 1997). Confidence in individual assignments was based on 10 000 simulations using Monte Carlo resampling methods developed by Paetkau et al. (2004). The rejection level was set at $p < 0.01$. Because of heterozygote deficiency across most populations, *dlu*4296 (shorthead redhorse) and *dlu*45 (river redhorse) were not included in simulations.

Results

Genetic diversity and disequilibrium

The microsatellite loci utilized in this study were moderately to highly polymorphic for both river redhorse and shorthead redhorse (Tables 1 and 2). Allele size frequencies for each microsatellite locus and population are presented in Supplemental Appendices S1–S4.[2] Tests of heterozygote deficiency showed deviations from HWE in 12%–25% of the population–locus combinations. Deviations were not consistent across loci within populations, but instead were associated with individual loci across most populations sampled. The following loci were consistently out of HWE: *dlu*45 (river redhorse: six Trent River and six Muskegon River populations); *dlu*4184 (shorthead redhorse: seven Muskegon River populations); *dlu*4296 (shorthead redhorse: 10 Trent River and six Muskegon River populations); and RR55 (river redhorse: five Muskegon River populations).

Linkage disequilibrium among pairs of loci tested within each population was present in less than 2.2% of combinations. No loci pair or within-population trends were evident. After pooling populations, linkage disequilibrium occurred for a greater percentage of combinations, mostly associated with the Trent River. For Trent River samples, linkage disequilibrium occurred at 22% of river redhorse and 24% of shorthead redhorse loci combinations. For Muskegon River samples, linkage disequilibrium occurred at 5% of river redhorse and 7% of shorthead redhorse loci combinations.

Allelic richness of Muskegon River redhorse was significantly greater than that of redhorse sampled from the fragmented Trent River (randomization test: river redhorse $p = 0.027$; shorthead redhorse $p = 0.001$). In contrast, observed heterozygosity was not significantly different between rivers (randomization test: river redhorse $p = 0.21$; shorthead redhorse $p = 0.52$). Genetic diversity of shorthead redhorse populations in the Trent River was significantly greater than that of river redhorse (one-tailed paired t test: A_R, $t = 3.56$, df = 9, $p = 0.003$; H_O, $t = 2.47$, df = 9, $p = 0.018$). For the Muskegon River, only shorthead redhorse allelic richness was significantly greater than river redhorse (one-tailed paired t test: A_R, $t = 12.4$, df = 6, $p < 0.0001$; H_O, $t = -0.68$, df = 6, $p = 0.26$).

Table 2. Site details and associated measures of genetic diversity for river redhorse (*Moxostoma carinatum*) and shorthead redhorse (*Moxostoma macrolepidotum*) sampled from the Muskegon River, Michigan.

		M. carinatum			*M. macrolepidotum*		
Site	rkm[a]	n	A_R	H_O	n	A_R	H_O
MA	22.8	12	6.54	0.79	47	12.90	0.76
MB	37.5	7	7.01	0.77	18	13.55	0.82
MC	53.8	28	6.84	0.75	48	13.04	0.74
MD	62.2	—	—	—	50	12.89	0.78
ME	66.1	34	6.93	0.77	48	13.68	0.76
MF	77.4	47	6.98	0.79	45	13.09	0.73
MG	87.7	30	6.89	0.75	43	13.09	0.80
MH	90.3	38	7.15	0.80	48	13.06	0.75
All		196	7.30	0.77	347	13.55	0.76

Note: See Fig. 1 for site locations. A_R, standardized allelic richness; H_O, observed heterozygosity.

[a]River kilometres (rkm) is the distance in kilometres upstream from river mouth.

The amount of genetic variability attributed to among-population differences was greater in the fragmented Trent River than in the Muskegon River (Table 3). However, AMOVA indicated that most genetic variability occurred within populations rather than among populations. For both species and rivers, allelic richness was significantly different among loci (Shapiro–Wilk: $p > 0.05$; ANOVA: $F = 43.1$ to 74.5, $p < 0.001$), but not among sites (Shapiro–Wilk: $p > 0.05$; ANOVA: $F = 0.08$ to 0.25, $p > 0.05$). Additionally, no significant differences in A_R and H_O were detected between different fragment length classes (randomization test: p values > 0.16). Shorthead redhorse heterozygosity in the Trent River was positively correlated with maximum spring CPUE ($r_S = 0.68$, $p = 0.047$) but not with river fragment length or distance upstream from river mouth. Other correlations between genetic diversity measures and fragment length, maximum spring CPUE, and distance upstream from river mouth were not significant ($p > 0.05$).

Evidence of recent population bottlenecks was not detected within fragmented Trent River populations. Wilcoxon signed-rank tests for heterozygote excess were not significant (p values = 0.79–0.99), indicating no significant departure from mutation–drift equilibrium. For both species, M was greater (river redhorse, 0.70–0.80; shorthead redhorse, 0.74–0.92) than the threshold value ($M < 0.68$) proposed by Garza and Williamson (2001). Values for Trent River populations were equal to or greater than those calculated for the unfragmented Muskegon River (river redhorse, 0.69–0.73; shorthead redhorse, 0.74–0.87). For Trent River redhorse populations, simulations based on the mean (p values > 0.09) and variance (p values > 0.25) of relatedness estimates

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Table 3. Analysis of molecular variance (AMOVA) results and global F_{ST} values for river redhorse (*Moxostoma carinatum*) and shorthead redhorse (*Moxostoma macrolepidotum*) populations in the Trent and Muskegon rivers.

River	Species	Individual (%)	Population (%)	Φ	p value	Global F_{ST}
Trent	*M. carinatum*	94	6	0.059	0.0001	0.034
	M. macrolepidotum	98	2	0.025	0.001	0.014
Muskegon	*M. carinatum*	99	1	0.012	0.002	0.007
	M. macrolepidotum	99	1	0.008	0.001	0.009

Note: Percent distribution of allelic diversity among individuals within populations and among populations is presented.

Table 4. Summary of pairwise tests of genetic differentiation among Trent River river redhorse (*Moxostoma carinatum*; below diagonal) and shorthead redhorse (*Moxostoma macrolepidotum*; above diagonal) populations.

	TA	TB	TC	TF	TG	TH	TI	TJ
TA		0.009	0.009	0.013	0.008	0.014	0.005	0.026
TB	—		0.024	0.027	0.022	0.034	0.015	0.041
TC	**−0.002**			0.005	**0.003**	0.010	0.010	0.020
TF	0.019	—	0.025		**0.001**	0.006	**0.005**	0.019
TG	—	—	—	—		0.008	0.007	0.014
TH	0.029	—	0.034	**0.008**	—		0.012	**0.006**
TI	0.035	—	0.035	0.035	—	0.064		0.023
TJ	0.046	—	0.051	0.047	—	0.079	0.013	

Note: See Fig. 1 for population locations. Nonsignificant intraspecific pairwise differences (after Bonferroni correction) are presented in bold type. Values are significant at $p < 0.0033$ (river redhorse) and $p < 0.0019$ (shorthead redhorse).

Table 5. Summary of pairwise tests of genetic differentiation among Muskegon River river redhorse (*Moxostoma carinatum*; below diagonal) and shorthead redhorse (*Moxostoma macrolepidotum*; above diagonal) populations.

	MA	MC	MD	ME	MF	MG	MH
MA		**0.002**	0.014	0.009	0.008	0.015	**0.003**
MC	—		0.016	0.010	0.006	0.014	0.006
MD	—	—		0.007	0.013	0.010	0.008
ME	—	0.014	—		**0.005**	**0.002**	**0.003**
MF	—	0.010	—	**0.002**		0.012	0.004
MG	—	0.014	—	**<0.001**	**0.002**		**0.005**
MH	—	0.016	—	**0.005**	0.008	0.007	

Note: See Fig. 1 for population locations. Nonsignificant intraspecific pairwise differences (after Bonferroni correction) are presented in bold type. Values are significant at $p < 0.005$ (river redhorse) and $p < 0.0024$ (shorthead redhorse).

did not indicate that relatedness among individuals sampled was greater than that expected from a random population sample.

Population structure

Pairwise F_{ST} tests identified weak but statistically significant population structure in both rivers. Greater population subdivision was detected along the fragmented Trent River than in the Muskegon River (Tables 4 and 5): 86% of Trent River pairwise comparisons were significantly different, whereas fewer Muskegon River pairwise comparisons were significantly different (river redhorse, 60%; shorthead redhorse, 71%). Global F_{ST} values for Trent River redhorse populations were 1.5 times greater (shorthead redhorse) and five times greater (river redhorse) than for Muskegon River redhorse (Table 3). Only the difference between river redhorse global F_{ST} estimates was significantly different between rivers (randomization test: $p = 0.048$). For both Trent River species, neighbour-joining dendrograms (not shown) supported the level of differentiation identified by pairwise F_{ST} comparisons and indicated that population structuring reflects the geographic proximity of populations. Dendrograms of Muskegon River populations (not shown) indicated less structuring for river redhorse than in the Trent River but a similar pattern for shorthead redhorse (Reid 2007).

Along the Trent River, population differentiation was significantly greater for river redhorse than for shorthead redhorse (one-tailed paired t test: F_{ST}, $t = -1.93$, df = 14, $p = 0.04$; D_{CE}, $t = -4.02$, df = 14, $p < 0.001$). Alternatively, for the Muskegon River, there was no difference between the two redhorse species (one-tailed paired t test: F_{ST}, $t = -0.61$, df = 9, $p = 0.28$; D_{CE}, $t = -1.14$, df = 9, $p = 0.14$).

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Fig. 2. Scatterplots of pairwise F_{ST} values versus (*a*) geographic distance and (*b*) number of dams separating pairs of Trent River populations of river redhorse (*Moxostoma carinatum*; solid circles) and shorthead redhorse (*Moxostoma macrolepidotum*; open squares).

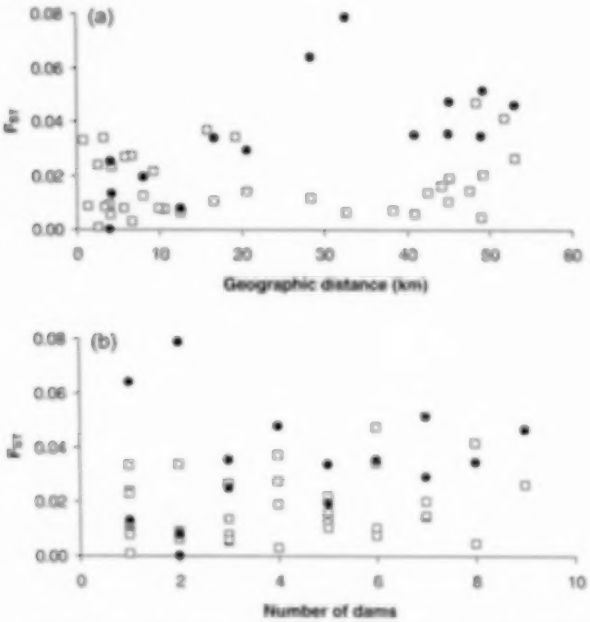
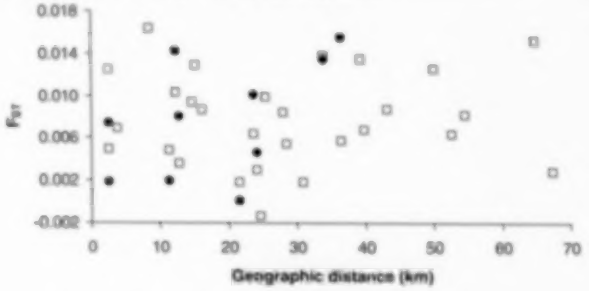


Fig. 3. Scatterplots of pairwise F_{ST} values versus geographic distance separating pairs of Muskegon River populations of river redhorse (*Moxostoma carinatum*; solid circles) and shorthead redhorse (*Moxostoma macrolepidotum*; open squares).



An isolation-by-distance (IBD) relationship was identified for river redhorse population pairs along the Trent River (Mantel test: F_{ST}, $Z = 17.8$, $r = 0.63$, $p = 0.049$; D_{CE}, $Z = 139.9$, $r = 0.48$, $p = 0.05$), but not for the other species–river combinations. There were no significant relationships between pairwise F_{ST} and D_{CE} values and the number of intervening dams. The significant IBD relationship suggests a balance between gene flow and drift for river redhorse populations in the Trent River (Hutchison and Templeton 1999, case I). Alternatively, scatterplots of F_{ST} values against geographic distance (Figs. 2 and 3) suggest that Muskegon River redhorse populations and Trent River shorthead redhorse populations are not in regional equilibrium and that gene flow is more influential than drift (Hutchison and Templeton 1999, case I). In all iterations of the two runs (70 000 per run), *I* (parameter estimated by 2mod) indicated that a migration–drift equilibrium model was more likely than a non-equilibrium drift-only model.

Individual assignment tests were unable to provide support for source–sink population dynamics along the Trent River. Despite population subdivision along the Trent River, only a small number of individual river redhorse or shorthead redhorse from hypothesized source populations were assigned back to their collection sites (Table 6). Accordingly, GeneClass was unable to assign individuals from putative sinks to hypothesized source populations.

Discussion

Genetic diversity and linkage disequilibrium

As predicted, redhorse genetic diversity in the fragmented Trent River was lower than that along the free-flowing reach of the Muskegon River. However, there was little evidence of recent population bottlenecks, among-site differences in diversity, or a relationship between genetic diversity and river fragment length. River fragmentation effects on genetic diversity have not been consistent across studies. Relative to below-dam populations, lower genetic diversity has been measured in headwater populations of river sculpin (*Cottus gobio*) (Hanfling and Weetman 2006) and white-spotted charr (*Salvelinus leucomaenis*) isolated by dams (Yamamoto et al. 2004). Conversely, no differences were detected among fragmented populations of black redhorse (*Moxostoma duquesnei*) (Reid et al. 2008) and several salmonid species (Neraas and Spruell 2001; Heggenes and Roed 2006; Deiner et al. 2007). Differences among study findings likely reflect variation in the duration of isolation, river fragment length, permeability of dams to gene flow, and species susceptibility to fragmentation effects. Additionally, these studies did not compare fragmented and free-flowing rivers. Without Muskegon River data, interpretation of fragmentation effects on the genetic characteristics of Trent River populations would have been limited.

Along the Trent River, redhorse population size was positively correlated with fragment length. However, in contrast to theoretical expectations, genetic diversity was not lower in small fragments. Only indirect evidence of a fragment size effect was provided through the correlation of shorthead redhorse observed heterozygosity with spawning run size. A habitat fragment size effect on genetic diversity has been shown for Lahontan cutthroat trout (*Oncorhynchus clarkia henshawi*; Neville et al. 2006) but not other stream-dwelling salmonids (Yamamoto et al. 2004; Whiteley et al. 2006). Explanations for the absence of any relationship include the following: (*i*) fragmentation was not sufficiently severe or long enough, (*ii*) gene flow was high enough to limit loss of genetic variation, (*iii*) habitat size alone is not a good predictor of population size and therefore genetic diversity, and (*iv*) non-equilibrium population dynamics (i.e., recent population declines or expansions) (Yamamoto et al. 2004; Dhuyvetter et al. 2005; Whiteley et al. 2006). If fragmentation of the Trent River has produced source–sink population dynamics, the genetic character of sinks will mimic source populations when persistence times for sink populations are short and (or) immigration events are common (Gaggiotti and Smouse 1996).

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Table 6. Summary of the number of individual redhorse (river redhorse (*Moxostoma carinatum*); shorthead redhorse (*Moxostoma macrolepidotum*)) correctly re-assigned by GeneClass (Cornuet et al. 1999) to their putative Trent River source populations.

	Population						
Species	TA	TC	TF	TG	TH	TI	TJ
M. carinatum	2/41 (4.9%)	0/47 (0%)	0/47 (0%)	—	2/48 (4.2%)	0/56 (0%)	0/35 (0%)
M. macrolepidotum	2/48 (4.2%)	2/51 (3.9%)	0/54 (0%)	2/57 (3.5%)	1/53 (1.9%)	1/55 (1.8%)	0/30 (0%)

Note: See Fig. 1 for population locations. Numbers of individual are presented as fractions of local sample sizes (percentages are provided within parentheses).

Measures of genetic diversity for both redhorse species were similar to those reported for Sacramento sucker (*Catostomus occidentalis*) (Whitehead et al. 2003), copper redhorse (*M. hubbsi*) (Lippe et al. 2006), and black redhorse (*M. duquesnei*) (Reid et al. 2008) and greater than that reported by DeWoody and Avise (2000) for most freshwater fishes. The relative insensitivity of catostomids to factors hypothesized to negatively affect genetic diversity may be related to their relatively late age of maturity and long life span (Whitehead et al. 2003; Lippe et al. 2006). In the Trent River, river redhorse begin to mature at age 6 and live up to at least 27 years. Shorthead redhorse begin to mature at age 4 and live up to at least 19 years (Reid 2006, 2007). The effects of genetic drift or population decline are expected to increase with each generation. Therefore, over the same period, river redhorse and shorthead redhorse would be less affected by rapid population declines and isolation than fishes with shorter generation times and life spans (e.g., river sculpin; Hanfling and Weetman 2006).

Linkage disequilibrium at the total population level (all populations combined) in the fragmented Trent River was substantially greater than in the Muskegon River. Linkage disequilibrium has been predicted to occur as a result of inbreeding, population bottlenecks, population admixture, population subdivision, and extinction–recolonization population dynamics (Ohta 1982*a*, 1982*b*; McVean 2002). To date, only a few studies investigating habitat fragmentation or regional population structure have reported increased linkage disequilibrium (Stewart et al. 1999; Tero et al. 2003; Zartman et al. 2006). As population persistence in small Trent River fragments is dependent on emigration from larger fragments (i.e., source–sink dynamics), greater linkage disequilibrium could result from extinction–recolonization dynamics.

Population structure

Higher global F_{ST} values indicate greater population subdivision in the fragmented Trent River than along the free-flowing reach of the Muskegon River. However, pairwise genetic distance estimates were not correlated with the number of intervening dams, and F_{ST} values for Trent River population pairs were much lower than those reported for other fragmented riverine fish populations (Meldgaard et al. 2003; Yamamoto et al. 2004; Hanfling and Weetman 2006). The moderate effect of fragmentation is likely the result of navigational locks that facilitate some upstream and downstream movement and gene flow by redhorse (Reid 2007).

Evidence supporting a non-equilibrium population model (source–sink or classic metapopulation) to describe redhorse population dynamics along the Trent River was provided by linkage disequilibrium at the total population level (indicative of extinction–recolonization dynamics) and the absence of an isolation-by-distance relationship for shorthead redhorse (no migration–drift equilibrium). Non-equilibrium conditions have also been reported for sets of plant and insect populations linearly distributed along rivers (Tero et al. 2003; Dhuyvetter et al. 2005; Liu et al. 2006). Of the two non-equilibrium models, demographic data supports source–sink dynamics as population persistence in small river fragments is dependent on migrants from larger fragments. However, predicted genetic diversity differences between small and large fragments were not observed. Differences among Trent River fragments can be expected to be limited if persistence times for sink populations are short and (or) immigration events are common (Gaggiotti and Smouse 1996) and if several potential source populations all contribute to the genetic diversity of sinks (migrant pool mode; Slatkin 1977).

Individual assignment tests were not able to assign individuals sampled from hypothesized Trent River sink populations to potential source populations, or conclusively reassign individuals sampled from potential source populations back to their collection sites. The ability of Bayesian assignment methods to correctly identify migrants and the number of populations is affected by the level of gene flow among populations, the number of individuals sampled within each population, and the number of genotyped loci (Cornuet et al. 1999; Waples and Gaggiotti 2006). Global F_{ST} estimates for river redhorse (θ = 0.034) and shorthead redhorse (θ = 0.014) in the Trent River indicate low population differentiation. High assignment probabilities require either greater levels of population differentiation ($F_{ST} > 0.1$; Manel et al. 2002) or more loci than were genotyped in this study (13 loci (Berry et al. 2004); 20+ loci (Cornuet et al. 1999)).

Gene flow between source and sink populations is expected to be unidirectional. Instead, mark–recapture data indicate movement among small fragments and from small fragments to larger ones (Reid 2007). This pattern could explain the lack of difference in genetic diversity among fragments and the inability of assignment tests to assign individuals to hypothesized source populations. Alternatively, rather than being sink populations, small fragments may function as migratory corridors or matrix habitat (Fahrig 2003) between populations in larger fragments.

Species differences in fragmentation effects

As predicted, shorthead redhorse populations were characterized by greater genetic diversity and less differentiation than river redhorse. This pattern could result from species-level differences in population size, habitat specialization, and proximity to the core of the species range. During the spawning period, the number of shorthead redhorse (aver-

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aged across populations) captured during boat-electrofishing was two (Trent) and five (Muskegon) times greater than river redhorse (Reid 2007). For neutral DNA markers like microsatellites, the expected level of polymorphism is proportional to effective population size. Populations of abundant species are expected to have greater genetic diversity (Bazin et al. 2006), and the loss of alleles through genetic drift is most likely in small isolated populations (Frankham 1996; Yamamoto et al. 2004). Therefore, fragmented populations of the more abundant shorthead redhorse would be less susceptible than river redhorse to genetic drift and the corresponding increase in population differentiation.

Based on Wright's island model, it has been proposed that only a few migrants (~1–10 per generation) between subdivided populations are required to maintain genetic diversity (Mills and Allendorf 1996; Frankham et al. 2002). If the likelihood of movement by individual river redhorse and shorthead redhorse between fragments can be considered equal, a larger number of migrants would be exported from shorthead redhorse populations, increasing the chance of meeting the threshold number of migrants. As Wright's island model also predicts that larger populations require fewer migrants to arrest divergence than smaller ones (Wang 2004), the likelihood of divergence among shorthead redhorse populations would be further reduced.

As a result of reduced availability of preferred habitats or hosts, populations of specialist species are often smaller and more isolated than habitat generalists and, correspondingly, have lower neutral genetic variation (Zayed et al. 2005). River redhorse is primarily found in the large rivers of the Laurentian Great Lakes basin. In the Lake Ontario and Lake Michigan basins, it is only found in the Trent River and in the Fox, Grand, Muskegon, and St. Joseph rivers, respectively. Compared with shorthead redhorse, which is widely distributed across rivers and lakes in the Great Lakes basin (Mandrak and Crossman 1992; Hubbs and Lagler 2004), there is less opportunity to maintain genetic diversity through gene flow. Heithaus and Laushman (1997) found differences in genetic diversity among co-occurring riverine fishes to be related to ecological specialization and corresponding sensitivity to pollution events. Based on different associations with free-flowing riverine habitats, the magnitude of fragmentation effects was predicted to differ between redhorse species. However, the effect on genetic diversity was similar, and between-species differences in genetic diversity were measured in both rivers. Additionally, fragmentation had similar effects on movement among fragments and population demographics (Reid 2007). Therefore, species-level differences in genetic diversity and population subdivision are more likely the result of habitat specialization effects on population size than different demographic responses to river fragmentation.

Based on geographic isolation, greater temporal variability in population size, and smaller effective population sizes, species at the periphery of their geographic range are expected to have low within-population genetic diversity (Lesica and Allendorf 1995). Reduced diversity has been reported for Arctic grayling (*Thymallus arcticus arcticus*; Stamford and Taylor 2004) and bull trout (*Salvelinus confluentus*; Whiteley et al. 2006) populations at the extremes of their North American ranges. In this study, river redhorse populations are isolated and at the northern periphery of the species' range. Alternatively, shorthead redhorse is widely distributed across the Laurentian Great Lakes basin and close to the core of its geographic range (Mandrak and Crossman 1992; Scott and Crossman 1998). In regards to population size and proximity to other populations at a regional level, differences between core and peripheral populations and between habitat generalists and specialists are similar (Vucetich and Waite 2003; Zayed et al. 2005). In this study, the relative influence of either phenomenon on genetic diversity and population structure could not be separated as river redhorse is a habitat specialist at the northern edge of its range and shorthead redhorse is a habitat generalist near the core of its range.

Future research

In this study, redhorse life-history characteristics and the permeability of the dam and lock system likely mitigated fragmentation effects. A broader understanding of the genetic consequences of river fragmentation requires further research on (*i*) smaller-bodied fishes with more limited dispersal patterns and shorter generation times (e.g., longnose dace, *Rhinichthys cataractae*), (*ii*) rivers fragmented by large hydroelectric or flood-control dams that present more substantial barriers to movement, and (*iii*) the effect of restored connectivity (e.g., dam removal) on previously fragmented populations. The inclusion of demographic and movement data and reference populations in future studies will support more conclusive inference (McElroy et al. 2003; Wilson et al. 2004; Johansson et al. 2006) and reduce the likelihood of false interpretations of fragmentation effect (Whitehead et al. 2003).

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Dispersal limitation and climate-related environmental gradients structure microcrustacean composition in freshwater lakes, Ellesmere Island, Canada

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Abstract: Dramatic environmental change is expected in the Arctic, yet little is known about the occurrence and community composition of microcrustaceans in Arctic lakes and how this will be influenced by future environmental change. We sampled and calculated relative abundances of microcrustacean species in 54 lakes on Ellesmere Island, Canada. New species records on Ellesmere Island included *Daphnia umbra*, *Tachidius discipes*, and *Artemeopsis stefanssoni*. *Daphnia middendorffiana/tenebrosa* was the most common taxon and often dominated microcrustacean assemblages, likely a result of its pigmentation, which offers resistance to ultraviolet radiation. Species richness was positively associated with nutrients, dissolved organic carbon (DOC), temperature, calcium, and conductivity and negatively affected by elevation. In contrast to most findings in temperate systems, we detected a negative relationship between species richness and surface area. Community composition was influenced by DOC, nutrients, and elevation but was also related to spatial variables, suggesting that spatial gradients in environmental conditions and dispersal are important drivers of differences among sites. Arctic ecosystems are expected to change rapidly in the coming years because of climate change and ozone thinning, and we expect that associated changes in DOC, temperature, and nutrients will affect microcrustacean species richness and distribution throughout the landscape.

Résumé : On s'attend à des changements environnementaux spectaculaires dans l'arctique; on connaît, cependant, assez mal la présence et la composition des communauté des microcrustacés des lacs arctiques et comment elles seront influencées par les futurs changements climatiques. Nous avons échantillonné les espèces de microcrustacés dans 54 lacs de l'île d'Ellesmere, Canada, et nous en avons déterminé les abondances relatives. *Daphnia umbra*, *Tachidius discipes* et *Artemeopsis stefanssoni* sont des espèces signalées pour la première fois sur l'île d'Ellesmere. *Daphnia middendorffiana/tenebrosa* est le taxon le plus commun et il domine souvent les peuplements de microcrustacés, vraisemblablement à cause de sa pigmentation qui lui procure une résistance à la radiation ultraviolette. La richesse spécifique est en corrélation positive avec les nutriments, le carbone organique dissous (DOC), la température, le calcium et la conductivité et en relation négative avec l'altitude. Contrairement à ce qu'on observe la plupart du temps dans les systèmes tempérés, nous détectons une relation négative entre la richesse spécifique et la surface du lac. La composition de la communauté est affectée par le DOC, les nutriments et l'altitude, mais il y a aussi une relation avec les variables spatiales, ce qui fait croire que les gradients spatiaux des conditions du milieu et de la dispersion sont d'importants facteurs explicatifs des différences entre les sites. On croit que les écosystèmes arctiques vont changer rapidement au cours des prochaines années à cause du changement climatique et de l'appauvrissement de la couche d'ozone et nous nous attendons à ce que les changements associés du DOC, de la température et des nutriments affectent la richesse spécifique et la répartition des microcrustacés dans tout le paysage.

[Traduit par la Rédaction]

Introduction

Relatively little information exists about the aquatic communities of the many hundreds of lakes throughout the High Arctic, with the exception of ongoing research on freshwater diatom assemblages (Douglas et al. 2004). Yet with increasing climate change, the Arctic is expected to be one of the most severely affected areas (International Arctic Science Committee 2005). Evidence based on paleolimnological studies suggests that biological communities in lakes and ponds in High Arctic regions have already experienced dramatic and unprecedented shifts in composition during the past 150 years, most likely associated with longer ice-free seasons and associated changes in lake productivity (Smol et al. 2005). In addition, recent research has revealed that chemical pollutants, including mercury and brominated flame retardants, are ubiquitous in Arctic lakes and biota (de Wit et al. 2006; Evans et al. 2006). To further our understanding of how these and other stressors will influence the structure and functioning of aquatic ecosystems, it is first necessary to determine what factors control the spa-

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tial distribution and local structure of Arctic aquatic food webs.

Microcrustaceans play a pivotal role in aquatic systems, transferring energy from primary producers to higher trophic levels. They likely have even greater ecological significance in the High Arctic, where food webs are simplified and the majority of lakes are fishless because of their shallow depth (Hershey et al. 2006). In addition, microcrustaceans are sensitive indicators of environmental conditions, as many species have short generation times and widely varying environmental preferences and tolerances. However, little is known about the species composition and distribution of microcrustaceans on Ellesmere Island in the Canadian High Arctic. The studies that have been done in this area have been mostly restricted to the Lake Hazen area. McLaren (1964) sampled microcrustaceans from Lake Hazen, as well as from a nearby pond, finding a total of eight microcrustacean species. A more wide-ranging survey (~38 km^2) was conducted by Røen (1981); however, this too was restricted to the Lake Hazen area, although 60 lakes were sampled and 22 species were collected. A more recent study of one lake and a fjord outside of the Lake Hazen basin found only two calanoid copepod species (Van Hove et al. 2001).

Microcrustaceans in temperate regions have been well studied, and a number of factors have been linked to their species richness and composition. These include primary productivity (Dodson 1992; Dodson et al. 2000), nutrient concentrations (Jeppesen et al. 2000; Sweetman and Smol 2006*b*), lake size (Dodson 1992), pH (Pinel-Alloul et al. 1990; Walseng et al. 2003), calcium, sulphate, and magnesium (Pinel-Alloul et al. 1995), total dissolved solids (Chengalath 1982), and predation (Keller and Conlon 1994). In addition, spatial factors relating to the distribution of lakes across the landscape may also affect microcrustacean community composition by influencing the dispersal of individuals between neighboring sites. Pinel-Alloul et al. (1995) divided variation into that explained by purely environmental variables (e.g., water chemistry), by purely spatial variables (e.g., a latitudinal gradient), and by spatially structured environmental variables (e.g., an environmental gradient across the study area) and found that although microcrustacean community composition depended on both environmental and spatial factors, purely spatial variables did not significantly increase the amount of variation that could be explained. However, Cottenie et al. (2003) detected a significant contribution of purely spatial variation in microcrustacean community composition but found that spatially structured environmental variation was minor, likely because their study area was small (2 km^2) compared with that of Pinel-Alloul et al. (1995) (3×10^5 km^2) and thus did not possess a strong environmental gradient. In addition, Beisner et al. (2006) found that space was a significant driver of microcrustacean community composition when both overland and watercourse distance were considered, suggesting that microcrustaceans may disperse equally well via water and aerial connections.

Although there have been relatively few studies in the Arctic compared with temperate regions, several studies of patterns in microcrustacean community structure have been conducted. Hebert and Hann (1986) surveyed microcrustacean communities across the North American Arctic from Churchill, Manitoba (58°47′N), to Polar Bear Pass, Nunavut (75°42′N), and from Cape Thompson, Alaska (165°46′W), to Frobisher Bay, Nunavut (68°30′W). They found 9–16 microcrustacean species in ponds in glaciated regions of the lower Arctic and 4–10 species in sites on islands in the Canadian High Arctic archipelago (Hebert and Hann 1986). A study of similar scope in the Yukon and western Northwest Territories found a total of 19 crustacean species, where abiotic variables (chloride, silica, and temperature) explained 25% of the variation in species composition (Swadling et al. 2000). A survey of 104 Alaskan Arctic lakes revealed that lake surface area and depth were important drivers of microcrustacean richness, whereas water chemistry and fish composition were insignificant (O'Brien et al. 2004). The Arctic undergoes periods of severe ozone depletion (Bottenheim et al. 2002). This is expected to worsen as atmospheric carbon dioxide levels rise (Austin et al. 1992), cooling the stratosphere and activating ozone-depleting compounds, suggesting that ultraviolet (UV) radiation may play an important role in high latitude locales. However, studies in the Arctic have failed to ascertain whether UV and UV-related factors (e.g., dissolved organic carbon (DOC)) influence microcrustacean community structure. In addition, none of these studies considered spatial variables as predictors in their analyses. Given the high number of lakes and ponds in Arctic regions, we expect that spatial variables (and therefore dispersal) will be important determinants of microcrustacean community structure.

For this study, we had three objectives: (*i*) to document microcrustacean species found in the northern third of Ellesmere Island; (*ii*) to determine what potential drivers are associated with species richness and community composition; and (*iii*) to investigate the relative importance of spatial versus environmental variables in determining species composition using powerful, newly developed statistical techniques, generally referred to as distance-based eigenvector maps (Borcard and Legendre 2002; Dray et al. 2006; Griffith and Peres-Neto 2006). In the past, spatial variables have been incorporated in ecological studies using polynomials of geographic coordinates (trend surfaces) (Borcard et al. 1992). However, this approach is not well suited to sampling in heterogeneous areas or irregular sampling designs and can only generate broad-scale spatial structures (Dray et al. (2006) and references therein). The advantage of distance-based eigenvector map techniques is that they offer flexibility in sampling design and are able to generate structures at a range of spatial scales (Borcard and Legendre 2002), allowing for the description of biological phenomena, such as seed dispersal, that may occur very locally or very broadly. Thus far, there has been little research aimed at understanding the controls on species richness and composition in the Canadian High Arctic and how they may differ from the trends found in temperate zones.

Materials and methods

Study site and sampling

Ellesmere Island (Fig. 1) is the northernmost landmass in Canada and is located in the High Arctic. Ellesmere is a region of continuous permafrost, where the winters are long and cold and the summer growing season lasts only 8–

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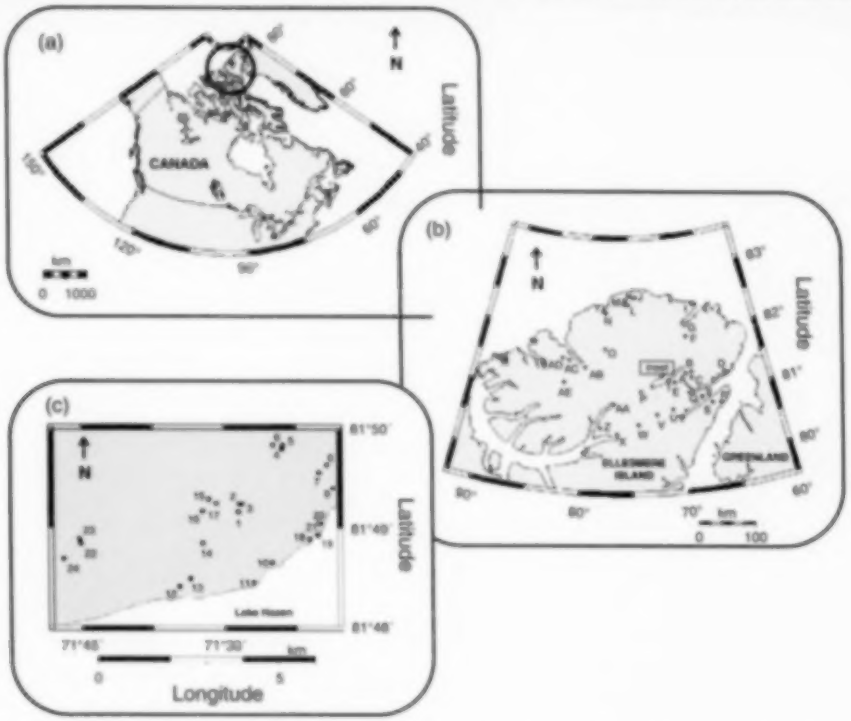
Fig. 1. Study location in (*a*) northern Canada, with sampling sites on (*b*) northern Ellesmere Island and (*c*) the Lake Hazen area.



12 weeks (Lévesque et al. 1997). Several glaciers remain, dominating the landscape and affecting the surface materials and climate of Ellesmere Island. Lake Hazen is a large lake north of 80°N latitude, and the area surrounding it is generally warmer and has more lush vegetation cover than other areas of Ellesmere Island (Keatley et al. 2007) because of protection from cold air flows by the surrounding mountain ranges.

Fifty-four lakes or ponds were sampled throughout the northern third of Ellesmere Island; waterbodies were named arbitrarily by the order in which they were sampled, and official lake names, locations, and morphometry are listed in Supplementary Table S1[2]. Samples were taken from 24 lakes in the Lake Hazen basin (81°49′N to 81°51′N), the lowlands immediately surrounding Lake Hazen. The remaining 30 samples were taken from lakes distributed over the northern third of Ellesmere Island (80°36′N to 83°05′N), primarily in the Grant Land Mountains region. A number of sites were located in coastal areas, and elevated calcium and conductivity values in these lakes likely indicate a marine influence (Supplementary Table S1).[2] However, the highest calcium and conductivity concentrations were observed in inland lakes around the polar oasis Lake Hazen, which in some sites may be due to the influence of the local bedrock but in others likely reflects increased evaporation due to warming, resulting in increased concentrations of solutes (Keatley et al. 2007).

Water samples for chemical and chlorophyll *a* analyses were taken by submerging a 1 L Nalgene® bottle below the water surface. Surface water temperature was measured near the shore using a handheld mercury thermometer. Conductivity and pH were measured using a portable Hanna® pHep 3 meter (Hanna Instruments Inc., Woonsocket, R.I., USA) and a YSI 33 conductivity meter (YSI Inc., Yellow Springs, Ohio, USA), respectively. Water samples were sent to Environment Canada's National Laboratory for Environmental Testing for analysis of major ions, nutrients, and metal concentrations (Environment Canada 1994) (Table 1; Supplementary Table S1).[2] A known volume of water was filtered through Whatman® GF/C filters (pore size 1.2 μm), which were then frozen in snow and kept in darkness for chlorophyll *a* analysis (Environment Canada 1994). Where sites were reached by helicopter, elevation was determined by altimeter. In other cases, elevation was estimated with maps from the National Topographic System of Canada (NTS) (Ottawa, Ontario). Length and width of each lake or pond were obtained from measurements using a laser distance finder or from the NTS maps. Lake surface area was estimated from width and length measurements using the formula for an ellipse. We were not able to access lakes by boat, and because of limited information about lakes in this area, mean and maximum lake depths are not available.

Microcrustaceans were collected between 6 and 18 July 2003 using a net (15 cm diameter, 80 μm mesh) fastened to

[2] Supplementary data for this article are available on the journal Web site (http://cjfas.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 3801. For more information on obtaining material refer to http://cisti-icist.nrc-cnrc.gc.ca/cms/unpub_e.html.

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Table 1. Median, range, and standard deviation (SD) of physical, chemical, and biological characteristics of all study lakes.

	Median	Range	SD
Elevation (m)	221	1–1006	244
Surface area (ha)	1.5	0.01–54 200	7370.9
Surface temp (°C)	12.5	0.5–22.0	5.7
Ice cover	0.0	0–1	0.4
pH	8.3	7.5–9.0	0.3
Conductivity ($\mu S \cdot cm^{-1}$)	174	30–1650	379
SiO_2 ($mg \cdot L^{-1}$)	1.64	0.13–13.90	3.40
Chlorine ($mg \cdot L^{-1}$)	1.46	0.12–32.4	7.43
Calcium ($mg \cdot L^{-1}$)	29.7	3.2–451	85.3
Chl *a* ($\mu g \cdot L^{-1}$)	0.50	0.1–1.6	0.42
TP ($\mu g \cdot L^{-1}$)	3.6	1.0–10.5	2.5
TN ($mg \cdot L^{-1}$)	0.33	0.06–1.99	0.56
DOC ($mg \cdot L^{-1}$)	4.5	0.6–40.1	11.0

Note: Abbreviations: chl *a*, chlorophyll *a*; TP, total phosphorus; TN, total nitrogen; DOC, dissolved organic carbon.

the end of a fishing rod. Several qualitative horizontal tows were taken from the surface waters within wading distance from the shore, as the ponds were too shallow to sample quantitatively. All lakes and ponds were sampled for approximately the same amount of time (i.e., similar sampling effort), and microcrustaceans were preserved in a ~4% formalin solution. In a comprehensive study of >2400 lakes in Norway, Walseng et al. (2006) found that there was a high degree of concordance in crustacean species identity in samples taken strictly from each of the littoral and pelagic zones, where all but two species found in pelagic samples were also found in littoral samples. Their study suggests that nearshore sampling can give an accurate assessment of microcrustacean assemblages in lakes and, thus, that our sampling effectively captured the diversity of microcrustacean taxa in lakes on Ellesmere Island. Additionally, both pelagic and littoral taxa are known to respond to environmental gradients (Walseng et al. 2003; Sweetman and Smol 2006*b*) and are therefore useful indicators of changing conditions in Arctic ecosystems.

Microcrustaceans were identified using a Leica MZ16 microscope (for microcrustacean relative abundance in study sites, see Supplementary Table S2)[2] and were generally identified to species, with the exception of juvenile stages, ostracods, and members of the family Chydoridae, the taxonomic affiliation of which is uncertain at northern latitudes in North America (Sweetman and Smol 2006*a*). Although Arctic *Daphnia* have genetic diversity that is comparable with that of temperate zone *Daphnia* (Hobaek and Weider 1999), genetic analysis was beyond the scope of this study, and thus, members of the Arctic *Daphnia pulex* group could not be identified as either *D. middendorffiana* or *D. tenebrosa*, as they showed similar morphological characteristics and are known to hybridize (Weider and Hobaek 2003). Henceforth, they will be referred to as *Daphnia middendorffiana/tenebrosa*. As well, *Bosmina freyi* and *Bosmina liederi* (DeMelo and Hebert 1994) are difficult to distinguish and, thus, will be referred to as *Bosmina freyi/liederi*. Two methods were used for counting the microcrustacean samples: samples with low abundances of microcrustaceans were counted in their entirety, whereas samples with greater abundances of microcrustaceans were halved multiple times using a Folsom plankton splitter, and fractions were counted in their entirety. The number of fractions counted was determined using species accumulation curves for each lake. Because sampling was not quantitative, microcrustacean relative abundances were calculated for each lake, both with juveniles included and excluded. Species richness, Shannon–Wiener diversity, and Simpson's measure of evenness ($E_{1/D}$) (Magurran 2004) were calculated from relative adult abundance. Higher values of both indices indicate greater diversity and evenness, and the maximum value of $E_{1/D}$ is 1.

Analyses

Multiple regression using the best subsets procedure in Statistica (version 6; StatSoft Inc. 2001) was used to determine which environmental variables explained patterns in species richness. Many of the environmental variables were significantly correlated, and thus, multicollinearity would have severely affected our results. Instead, we performed a principal components regression, which uses a principal components analysis (PCA) of environmental variables to generate linear combinations of variables, which are then used as explanatory variables in a multiple regression, removing the effects of multicollinearity (Graham 2003). By assessing the loadings of each environmental variable on the principal components axes, we were able to evaluate which variables were important predictors of species richness. Physical and chemical variables thought to be relevant to microcrustacean biology (i.e., calcium, total nitrogen (TN), total phosphorus (TP), DOC, conductivity, elevation, lake surface area, latitude, temperature) were selected for PCA, and the first four principal components were chosen for multiple regression analysis. Dissolved metal concentrations were not considered in the analysis as all were below the ranges found to be toxic in microcrustaceans (Baudouin and Scoppa 1974). Similarly, pH was excluded from analysis, as in all lakes, it was above the pH considered to be harmful to microcrustaceans (pH < 6.0; Marmorek and Korman 1993). Adjusted R^2, Mallows' C_p, and Akaike's information criterion (AIC) were used to evaluate the strength of the regression models.

Multivariate ordination techniques were used to assess patterns of species abundances using CANOCO (version 4.5; ter Braak and Šmilauer 2002). Similar to our multiple regression analyses, a reduced set of environmental variables thought to be relevant to microcrustaceans was chosen. Spatial variables were created by converting Cartesian coordinates (x, y) to a grid using a Lambert conformal conic projection, as UTMs (universal transverse mercator) become distorted in polar regions. Distance-based eigenvector maps were used to transform spatial coordinates to interpret the scale of spatial variation (Borcard and Legendre 2002; Dray et al. 2006; Griffith and Peres-Neto 2006). The transformation of a simple grid into more complex spatial variables at both fine and broader scales allows greater resolution of spatial variability in a sampling area. The program spacemakeR was used to create the eigenvector maps (Dray 2006) using the statistical language R (R Development Core Team 2006). A pairwise Euclidean distance matrix (d_E) was computed from the newly created Lambert projection coordi-

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nates of sampling sites and was transformed into a truncated connectivity matrix (**W**), defined by the threshold value t, where

$$\mathbf{W} = w_{ij} = \begin{cases} 0 & \text{if } i = j \\ 0 & \text{if } d_{ij} > t \\ [1 - (d_{ij}/\max(d_{ij})] & \text{if } d_{ij} \leq t \end{cases}$$

Thus, sites that are closer together are given greater weight in the analysis. The value t was determined by testing the neighbourhood connectivity of our sites by performing a Delaunay triangulation, Gabriel graph, relative neighbourhood graph, and sphere of influence (Legendre and Legendre 1998). By testing different neighbourhood connectivity methods, we are able to ascertain at what scale processes such as dispersal are operating, as different methods have differing levels of connectivity. For example, the Delaunay triangulation method had an average of five connections per site in the Lake Hazen area, with a large number of long-distance connections, whereas the relative neighbourhood method had an average of two connections per site, with more localized neighbourhoods and fewer long-distance connections. Fewer, more localized connections might be more important to microcrustaceans, which can disperse via water connections, wind, and waterfowl, all of which may be more important vectors at small spatial scales.

The spatial variables derived from each connectivity matrix were tested with the species abundances in an ordination. We then chose the connectivity method in which the spatial variables generated explained the greatest amount of variation, which was the relative neighbourhood method in all cases. Following this, eigenvectors were computed from the matrix **W**, with those associated with small eigenvalues representing local structures and those associated with large eigenvalues representing regional scales (Dray et al. 2006). As an example, some of the eigenvectors generated for the Lake Hazen sites are illustrated (Fig. 2), where the eigenvector representing the very broadest regional scale has two distinct clusters of sites (Fig. 2*a*) and each successive eigenvector has progressively more localized clusters of sites, culminating in the most fine-scale local spatial eigenvector (Fig. 2*d*). It is important to note that although the spatial variables generated have both positive and negative values, this simply separates sites into different clusters and, thus, does not represent positive or negative relationships.

We performed ordinations on a subset of sites (the Lake Hazen region) and on the entire set of lakes from Ellesmere Island. This allowed us to examine the species compositions at small scales (i.e., <10 km), where local factors such as dispersal would be expected to be greater than at larger scales, in contrast with the species compositions at larger scales (>300 km), where environmental gradients may be more important and dispersal would be limiting. Site EPI was excluded from ordinations as there were no organisms recovered in the sampling. All species and juvenile stages were included in our ordinations, as some of the lakes had only juveniles present. In addition, we tested the association of species with differing spatial scales following Brind'Amour et al. (2005), where we classified the spatial variables into scales of very broad, broad, meso, and fine based on groupings of their eigenvalues (e.g., Fig. 2). We will use this classification scheme throughout, referring to different spatial variables by their scale and number, e.g., **broad1** represents broad spatial scale variable 1. We chose only significant eigenvectors for the spatial submodels, tested each spatial submodel in a redundancy analysis (RDA), and then used the species loadings on the first canonical axis to interpret which species were most influenced by different spatial scales.

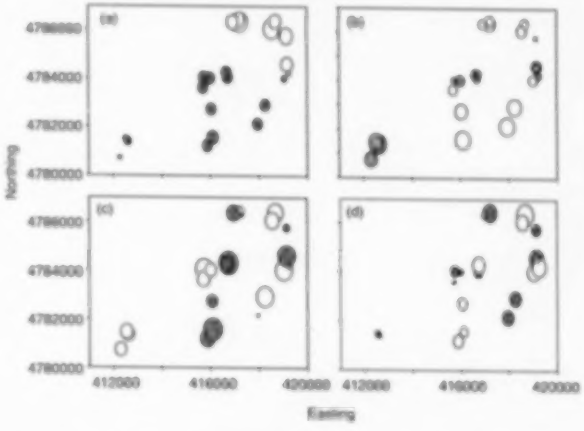

Fig. 2. Examples of spatial eigenvectors of the Lake Hazen site at progressively finer scales. Circles are plotted at sampling locations, where larger circles represent larger positive (shaded) or negative (open) values of the eigenvector. (*a*) Variable **very broad1** represents the largest regional-scale variability, (*b*) variable **broad2** represents broad-scale variability, (*c*) variable **meso2** represents intermediate- or meso-scale variability, and (*d*) variable **fine1** represents fine local-scale variability. Notice that at the very broad scale, sites are grouped into two clusters, with increasing numbers of clusters at progressively finer scales.

A detrended correspondence analysis was conducted on species abundances to assess the length of the environmental gradient, from which it was determined that RDA was appropriate. Species abundances were Hellinger-transformed to reduce the influence of rare species (Legendre and Gallagher 2001). We tested if there was a linear spatial gradient in species abundances, and it was removed from the whole Ellesmere Island set by taking the residuals of the x, y coordinates and species abundances. Forward selection with 499 Monte-Carlo permutations was used to determine which individual environmental and spatial factors had a significant impact on the community composition. Collinearity was detected if the variance inflation factor was >20 (ter Braak and Šmilauer 1998). Environmental variables that were not significant were plotted as supplementary values, which act passively and have no influence on the ordination diagram.

Variation partitioning techniques were used to determine the relative influences of purely environmental (*en*), spatially structured environmental (*sp-en*), and purely spatial (*sp*) variables on species distributions (Borcard et al. 1992). Canonical ordinations are biased by the number of predictor variables and sample size (Peres-Neto et al. 2006), so we employed the estimators of Peres-Neto et al. (2006) to control for this bias and to test the significance of the

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Table 2. Proportion of lakes and ponds occupied by crustacean taxa found in the Lake Hazen area and northern Ellesmere Island.

Taxonomic affiliation	Abbreviation	Lake Hazen area, Ellesmere Island	Northern Ellesmere Island
Subphylum Crustacea			
Class Branchiopoda			
Order Anostraca			
Branchinecta paludosa (O.F. Müller, 1788)	*B.palud*	0.63	0.20
Artemiopsis stefanssoni Johansen, 1921	*A.stefan*	0.04	0.07
Juvenile Anostraca	juv Anostr	0.21	0.07
Order Cladocera			
Daphnia middendorffiana/tenebrosa	*D.midden*	1.00	0.60
Daphnia umbra Taylor et al., 1996	*D.umbra*	—	0.03
Bosmina freyi/liederi DeMelo and Hebert, 1994	*B.frli*	0.13	0.13
Chydoridae	Chydorid	0.75	0.27
Holopedium gibberum Zaddach, 1855	*H.gibber*	0.04	—
Order Notostraca			
Lepidurus arcticus (Pallas, 1793)	*L.arct*	0.04	0.03
Juvenile Notostraca	juv Notostr	0.21	—
Class Maxillopoda			
Subclass Copepoda			
Order Calanoida			
Limnocalanus macrurus G.O. Sars, 1863	*L.macru*	—	0.03
Calanoid copepodid	cala cpd	0.08	0.23
Nauplii	nauplii	0.83	0.77
Order Cyclopoida			
Eucyclops agilis (Koch, 1838)	*E.agilis*	0.67	0.10
Megacyclops magnus (Marsh, 1920)	*M.magnus*	0.46	0.03
Cyclops scutifer G.O. Sars, 1863	*C.scutifer*	0.33	0.57
Cyclopoid copepodid	cycl cpd	0.96	0.63
Order Harpacticoida			
Tachidius discipes Giesbrecht, 1881	*T.discip*	—	0.03
Attheyella nordenskioldi (Lilljeborg, 1902)	*A.norden*	0.21	0.07
Harpacticoid copepodid	harp cpd	0.29	0.17
Class Ostracoda	Ostracod	0.46	0.17

variance fractions, as well as to test for significant differences between fractions.

Results

Fifteen taxa were identified from the lakes and ponds on northern Ellesmere Island (Table 2). The most frequently found microcrustacean taxa were *Daphnia middendorffiana/tenebrosa*, *Cyclops scutifer*, and Chydoridae. Species found in this study that had not previously been noted on Ellesmere Island included *Daphnia umbra* Taylor et al. 1996, *Artemiopsis stefanssonii* Johansen, 1921, and *Tachidius discipes* Giesbrecht, 1881. The frequency of occurrence for the various taxa ranged from 2% to 80% of lakes on Ellesmere, with *D. middendorffiana/tenebrosa* being the most common taxa. In general, most taxa occurred in a low number of lakes; however, taxa in the warmer Lake Hazen region tended to occur with greater frequency (Table 2).

Species richness varied from 0 to 9 taxa per lake, averaging 3.4 taxa per lake (Fig. 3). Species richness in the Lake Hazen area was significantly greater than in lakes in the rest of northern Ellesmere Island ($t = -4.73$, $p < 0.01$, df = 52). Principal component 1 (PC1) explained the majority of variation in species richness, with a small contribution from PC3 (Table 3). PC1 had high positive loadings with temperature, conductivity, calcium, DOC, TN, and TP and negative loadings with surface area, whereas PC3 had a high negative loading with elevation (Table 3). Species diversity, measured by the Shannon–Wiener index, was generally low in most lakes and positively skewed by a large number of small values (mean 0.45; median 0.36) (Fig. 3). Diversity was significantly greater in the Lake Hazen area than in northern Ellesmere ($t = -2.77$, $p < 0.01$, df = 52). Evenness (mean 0.46; median 0.41) (Fig. 3) was significantly greater in northern Ellesmere than in the Lake Hazen region ($t = 2.38$, $p = 0.01$, df = 52).

The overall RDA of all Ellesmere Island sampling sites was significant (trace = 0.39, $F = 4.82$, $p < 0.01$), and we found that the first axis was driven by productivity (TP), ice cover, and broad-scale spatial variation (**broad2**), differentiating between sites in the Lake Hazen region and sites on the rest of the island ($\lambda_1 = 0.28$, $F = 18.15$, $p < 0.01$) (Fig. 4). *Daphnia middendorffiana/tenebrosa* and *Branchinecta paludosa*, an anostracan, were positively associated with TP, whereas juvenile stage copepods were positively related to ice cover. The second axis ($\lambda_2 = 0.04$) was structured by elevation (likely a proxy for temperature and (or) isolation) and different meso-scale (**meso3**, **meso5**) spatial

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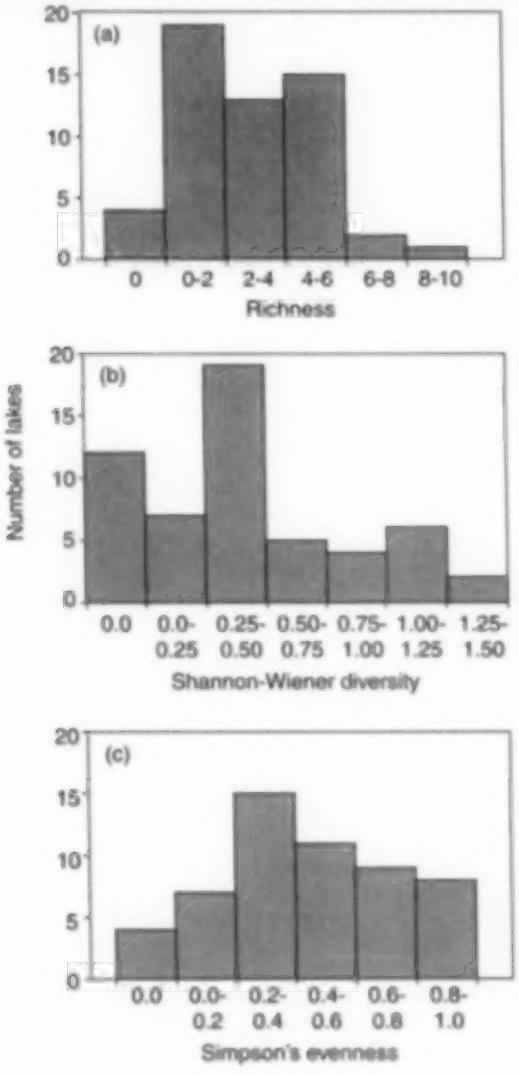
Fig. 3. (*a*) Richness, (*b*) Shannon–Wiener diversity, and (*c*) Simpson's evenness distributions in lakes on Ellesmere Island.



variables. Cyclopoid and harpacticoid copepods, bosminids, and chydorids were positively associated with elevation and were associated with the meso-scale spatial variables **meso3** and **meso5**.

The Lake Hazen area RDA was also significant (trace = 0.58, $F = 3.84$, $p < 0.01$); however, its first axis was controlled by DOC and elevation (Fig. 5). The variables TN and TP were highly correlated with DOC and were therefore removed as active variables in the analysis. DOC was positively associated with *D. middendorffiana/tenebrosa* and adult *B. paludosa*, whereas elevation was positively correlated with juvenile copepods and juvenile and adult anostracans ($\lambda_1 = 0.34$, $F = 8.91$, $p < 0.01$). The second axis ($\lambda_2 = 0.11$) was driven by spatial variables. Broad regional-scale variables **very broad2** and **very broad3**, as well as meso-scale variable **meso2**, were positively associated with several cyclopoid and harpacticoid copepod taxa, bosminids, chydorids, and juvenile notostracans. *Holopedium gibberum* and ostracods were positively correlated with meso-scale variable **meso1**. The supplementary environmental variables TN and TP were highly positively correlated with DOC in both the Lake Hazen area and all of Ellesmere, suggesting that DOC and nutrients are likely the most important variables in lakes on Ellesmere Island.

Species that are thought to be effective dispersers, such as the fairy shrimp (*Brachinecta paludosa*; Bohonak and Whiteman 1999) and the pigmented *D. middendorffiana/tenebrosa* (Mellors 1975), were highly correlated with broad spatial scales at the Lake Hazen region (Table 4). As an example, *D. middendorffiana/tenebrosa* was positively associated with the white sampling locations generated by broad-scale spatial variable **broad2** (Fig. 2*b*). In addition, *D. middendorffiana/tenebrosa* was also highly correlated with very broad and broad spatial variables at the larger Ellesmere Island scale. Most cladoceran taxa, juvenile notostracans, ostracods, and nauplii were correlated with very broad and broad spatial structures, suggesting that they have broad distributions. Several cyclopoid and harpacticoid copepod taxa were also highly correlated with very broad and broad spatial scales in both ordinations.

Variation in microcrustacean communities in the Lake Hazen area was mostly explained by purely environmental (*en*) and purely spatial (*sp*) variables, which contributed 29% and 21% of variation, respectively (Fig. 6). In contrast, purely spatial variables contributed very little to overall variation in microcrustacean composition at the larger Ellesmere Island scale (7%), whereas purely environmental variables explained a similar amount of variation at both scales (Ellesmere, 23%; Lake Hazen, 29%) (Fig. 6). Spatially structured environmental (*sp-en*) variables explained little variation at both scales (<4%). Pure spatial and pure environmental variation were significantly different from zero in the Lake Hazen and Ellesmere Island data sets (all variables: $p < 0.01$). As well, there was no difference between environmental and spatial variation at the Lake Hazen scale ($p = 0.60$), but environmental variables explained more variation than spatial variables in Ellesmere Island communities ($p = 0.04$).

Discussion

Our survey of lakes and ponds on northern Ellesmere Island revealed patterns of species richness and composition that are consistent with climate-induced environmental gradients and spatial structuring. Microcrustacean richness and distribution were correlated with variables that can be influenced by a warmer climate, such as greater nutrient and DOC concentrations resulting from increased terrestrial vegetation and greater conductivity as a result of evaporative concentration of solutes (Keatley et al. 2007). Additionally, microcrustaceans were structured by variables associated with dispersal limitations such as elevation. Although some of the common relationships between environmental variables and microcrustaceans that have been observed in temperate systems were also observed in our study, we found that other variables, such as DOC, can influence Arctic

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Table 3. (*a*) Multiple regression of principal component variables to predict species richness and (*b*) loading of environmental variables on principal components axes.

(*a*) Multiple regression of principal component variables to predict species richness.

	Adjusted R^2	C_p	AIC	*F* ratio	*p* value	Variable	Coefficient	Partial correlation coefficient	*t* value	*p* value
Model 1	0.39	1.28	59.55	18.23	<0.01*	PC1	0.62	0.63	5.84	<0.01*
						PC3	–0.16	–0.21	–1.53	0.13
Model 2	0.38	1.52	57.96	33.27	<0.01*	PC1	0.62	0.62	5.77	<0.01*

(*b*) Loading of environmental variables on principal components axes.

	PC1	PC2	PC3	PC4
Latitude	–0.3104	**–0.7551**	0.2853	–0.4111
Temperature	**0.8458**	0.0630	0.1103	0.0717
Conductivity	**0.8773**	0.2919	0.2069	0.0448
Calcium	**0.8379**	0.3512	0.1811	0.0890
Chl *a*	0.1707	**–0.7260**	0.0127	0.5826
DOC	**0.9297**	–0.1951	–0.0617	–0.1868
TN	**0.8540**	–0.1626	–0.1553	–0.3642
TP	**0.9018**	–0.2657	–0.0323	–0.1777
Elevation	0.0596	–0.0281	**–0.9742**	–0.0368
Surface area	*–0.6837*	0.2232	0.0921	–0.3592

Note: Smaller values of Mallows' C_p and Akaike's information criterion (AIC) indicate the most parsimonious model. Values in bold type indicate variables with high loadings (>0.7); values in italics indicate moderately high loadings. Abbreviations: chl *a*, chlorophyll *a*; DOC, dissolved organic carbon; TN, total nitrogen; TP, total phosphorus. *p* values followed by an asterisk (*) are significant at $p < 0.05$.

microcrustacean communities. We found evidence of spatial patterns, especially around Lake Hazen, where 21% of variation in species distributions was due to the structuring of communities by spatially related factors, which probably results from dispersal between nearby lakes. However, we also observed low frequencies of microcrustacean taxa and high beta diversity (Lande 1996), both at the Lake Hazen scale (59%) and for all the sites on Ellesmere (73%), suggesting that dispersal is limiting in the harsh landscape of the Arctic.

The main determinants of species richness and composition in our study were nutrients, conductivity (which was highly correlated with calcium), and DOC. Although lake productivity (Dodson et al. 2000; Jeppesen et al. 2000) and calcium (Wærvågen et al. 2002) are well-known predictors of microcrustacean species richness and composition in temperate zones, DOC is rarely a significant driver of microcrustacean community structure (Keller and Pitblado 1984; Hessen et al. 2006; but see Wissel et al. 2003). However, Olson et al. (1995) also found that DOC and colour were important predictors of zooplankton community composition in a chronosequence of lakes in Alaska, where increasing colour in older lakes altered competitive and predator–prey interactions. In Arctic lakes, DOC primarily results from allochthonous input from the surrounding watershed (Hamilton et al. 2001) and the humic content acts to reduce microcrustacean mortality due to UV radiation (Rautio and Korhola 2002*a*). In the Lake Hazen region, lakes have elevated concentrations of DOC and nutrients, probably resulting from the lush vegetation associated with warmer temperatures in the polar oasis (Keatley et al. 2007); however, lakes outside of this polar oasis had significantly lower DOC concentrations ($t = -4.92$, $p < 0.01$, df = 26). In shallow study lakes, we would expect that increased melanization would be the primary way in which microcrustaceans, such as *Daphnia middendorffiana/tenebrosa*, would avoid UV damage in low DOC lakes (Rautio and Korhola 2002*b*). However, we also expect *D. middendorffiana/tenebrosa* to do well in high DOC lakes where they would not produce as much melanin (Rautio and Korhola 2002*b*), and this energy could therefore be redirected towards growth and reproduction, increasing their competitive ability (Hessen 1996). In addition, DOC from terrestrial sources can serve as a food source for microcrustaceans (Carpenter et al. 2005). Indeed, we observed a wide range of *D. middendorffiana/tenebrosa* relative abundances at low DOC (<1%–100% of adults at DOC ≤ 5 mg·L^{-1}, mean = 46%) but higher relative abundances at high DOC (mean = 72%). The role of DOC in structuring microcrustacean communities is likely related to mechanisms of UV avoidance and possibly also food availability and would likely be important in other systems where UV light penetration is high, i.e., high elevation and boreal lakes and ponds. The success of *D. middendorffiana/tenebrosa* may also be due to a lack of fish predation, releasing it from the tradeoffs associated with its larger size and pigmentation. Although we do not have fish data available for our study lakes, many of the ponds probably freeze solid during the winter and, therefore, would not support fish populations.

Temperature, temperature-related variables, e.g., surface area, and elevation were secondary determinants of microcrustacean composition and richness. Lakes with large surface areas tend to be colder and take longer to heat than small lakes; thus there is an inverse relationship between temperature and surface area. Elevation is likely a proxy of both temperature and isolation, as its negative influence on

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Fig. 4. Redundancy analysis of microcrustacean communities from all sample sites on Ellesmere Island. (*a*) Species and (*b*) sample sites (Lake Hazen area, solid circles; northern Ellesmere, open circles) in relation to environmental and spatial variables. Species are represented by thin-line vectors and italic type (see Table 2 for abbreviations), environmental (see Table 1 for abbreviations) and spatial variables are represented by thick-line vectors and bold type, and supplementary environmental variables are shown with shaded, broken-line vectors and bold–italic type. Spatial variables are abbreviated: **broad2**, broad-scale variable 2; **meso3**, meso-scale variable 3; **meso5**, meso-scale variable 5.

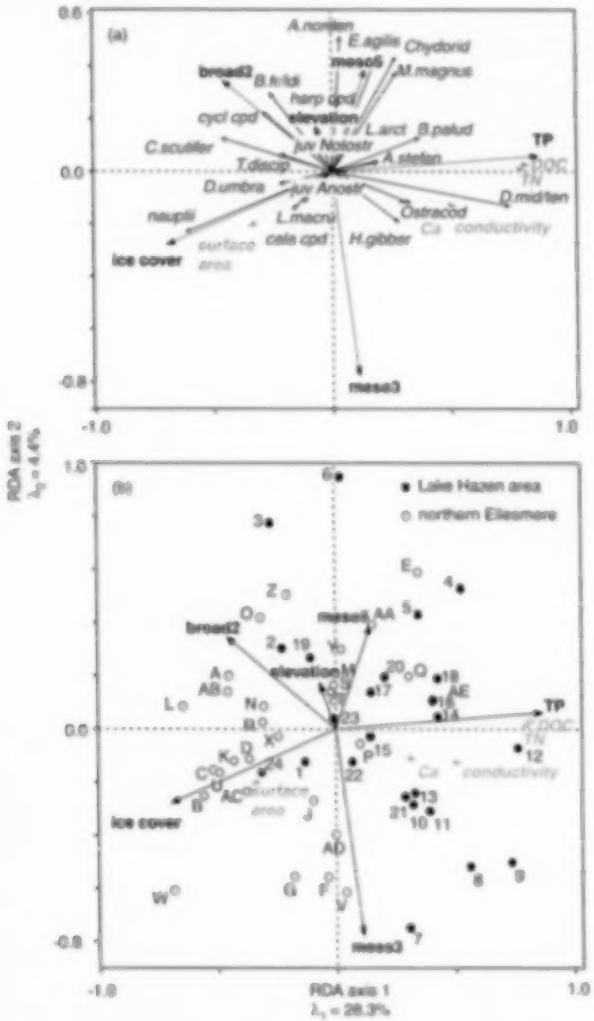
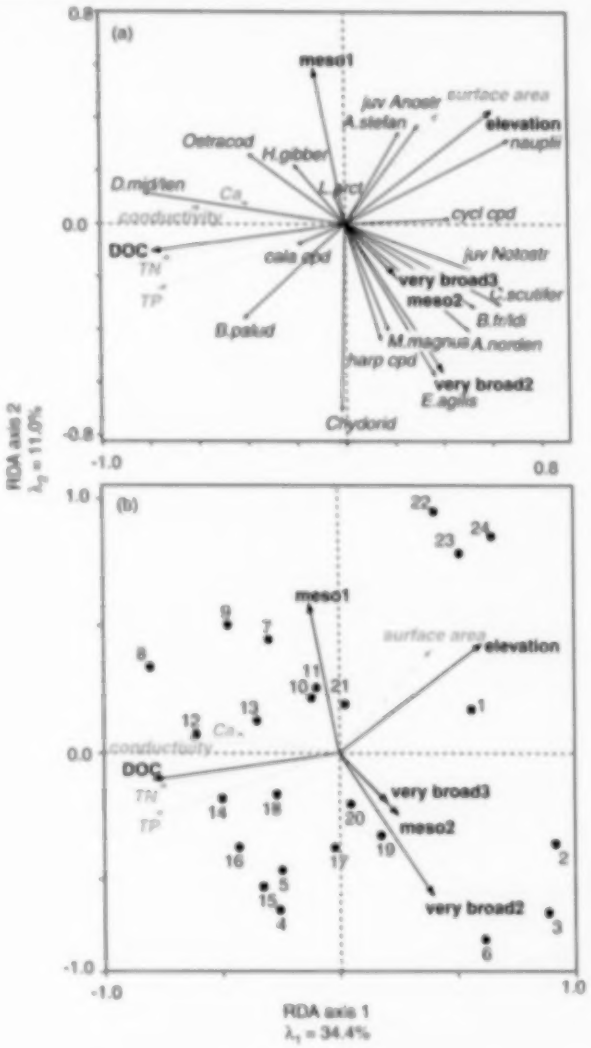


Fig. 5. Redundancy analysis of microcrustacean communities from sites around Lake Hazen. (*a*) Species and (*b*) sample sites in relation to environmental and spatial variables. Species are represented by thin-line vectors and italic type (see Table 2 for abbreviations), environmental (see Table 1 for abbreviations) and spatial variables are represented by thick-line vectors and bold type, and supplementary environmental variables are shown with shaded, broken-line vectors and bold–italic type. Spatial variables are abbreviated: **very broad2**, very broad-scale variable 2; **very broad3**, very broad-scale variable 3; **meso1**, meso-scale variable 1; **meso2**, meso-scale variable 2.



species richness and positive relationship with juvenile stages probably reflects fewer microcrustacean propagules from upstream sources, colder water temperatures, later ice-off dates, and thus, slower reproduction and development. Hessen et al. (2006) found that high-elevation lakes generally had low species richness, which they attributed to difficulties in colonization. In contrast to the positive relationship that is generally observed between surface area and microcrustacean richness in temperate lakes (Dodson 1992), we found a negative relationship between surface area and microcrustacean richness. Hessen et al. (2006) and Walseng et al. (2006) also failed to observe a positive relationship between area and crustacean species richness at high latitudes. As larger lakes hold more volume and take longer to heat, this suggests that temperature can override the positive effect of area on microcrustacean richness. We acknowledge that as a result of sampling near the shore, we

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Table 4. Species scores on canonical axis 1 for individual spatial submodels (spatial scale followed by spatial variable in parentheses).

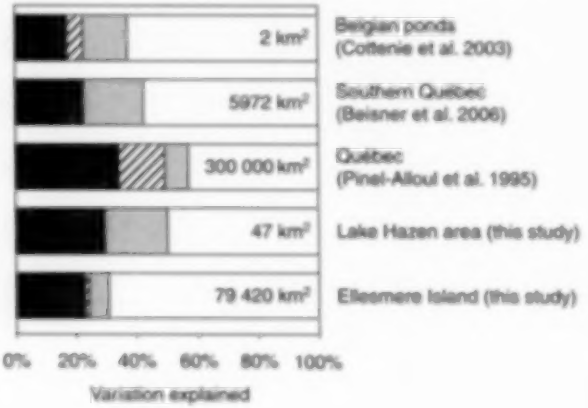
		Ellesmere	
	Lake Hazen, broad (**broad4–5**)	Very broad (**very broad1–2**)	Broad (**broad3–11**)
B.paliad	**–0.4856**	0.1828	–0.0555
A.stefan	**0.3758**	0.0662	0.0791
juv Anostr	**0.5675**	0.0277	–0.0435
D.midden	**–0.6034**	**0.3698**	**–0.5764**
D.umbru		–0.1306	*0.2609*
B.firfi	*0.2266*	0.0838	*0.2573*
Chydorid	**–0.3283**	*0.2734*	–0.0873
H.gibber	–0.0804	0.0534	*–0.2800*
L.arct	–0.1695	0.1023	–0.1379
juv Notostr	*0.2049*	**0.4294**	**0.3098**
L.macru		–0.0196	0.0669
cala cpd	*–0.2303*	–0.0487	0.1205
nauplii	**0.5117**	*–0.2887*	**0.4337**
C.scutifer	**0.3115**	–0.1738	*0.2772*
E.agilis	–0.0199	**0.6001**	0.1106
M.magnus	–0.1089	**0.4795**	–0.0152
cycl cpd	**0.4081**	–0.1202	0.0074
A.norden	0.1697	*0.2070*	0.1446
T.discip		–0.0935	0.0667
harp cpd	0.0019	0.0499	*0.2233*
Ostracod	–0.1154	0.0835	*–0.2009*

Note: Values in bold type indicate species with high loadings (>0.3); values in italics indicate moderately high loadings (0.2–0.3). Only significant spatial submodels are presented. Species abbreviations as in Table 2.

may have missed some hypolimnetic taxa in larger lakes, which would be reflected by lower species richness in larger lakes. However, the hypolimnetic *Cyclops scutifer* was detected in almost 50% of lakes, including several of the largest lakes (Supplementary Tables S1 and S2),[2] suggesting that our sampling was representative of the microcrustacean community in lakes on northern Ellesmere Island. Thus, high-latitude microcrustacean communities appear to be structured by different processes than temperate lake microcrustaceans, as in general, most environmental predictors showed significant variability, suggesting that our results are not an artefact of sampling a restricted range of environmental conditions.

With temperatures in the Arctic expected to rise by 3–5 °C by the end of the 21st century (International Arctic Science Committee 2005), consideration of the effect of warming on microcrustaceans in these lakes is of great importance. Temperature provides both direct, e.g., metabolic, and indirect, e.g., food availability, mechanisms for change in microcrustacean communities. This trade-off between higher production and increased metabolic demands will likely favour smaller species (Moore et al. 1996). This was observed experimentally where daphniid and overall zooplankton biomass declined in high-elevation experimental ponds when the temperature was raised, likely responding to temperature-induced changes in algal composition (Strecker et al. 2004). Although we observed some small-bodied microcrustaceans (e.g., chydorids) in warmer locations, in general, the large-bodied *Daphnia* dominated

Fig. 6. Comparison of variation explained in microcrustacean communities in Cottenie et al. (2003), Beisner et al. (2006), Pinel-Alloul et al. (1995), Lake Hazen, and Ellesmere Island. Variation in species abundances is explained by purely environmental (*en*, solid bars), spatially structured environmental (*sp-en*, hatched bars), and purely spatial (*sp*, shaded bars) variables, where the remaining variation is unexplained by the examined variables (open bars). Study areas are listed on right side of the graph.



assemblages in lakes with higher temperatures such as those found in the polar oasis Lake Hazen region (15.3 °C ± 4.9 °C in Lake Hazen sites versus 8.5 °C ± 4.7 °C in northern Ellesmere Island sites). This suggests that perhaps the thermal optimum of *Daphnia* has not yet been reached, but with increasing temperature, it will likely be vulnerable to higher metabolic costs.

Temperature also affects reproduction directly by accelerated development (Moore et al. 1996) and indirectly by increasing the length of the growing season. Hebert and Hann (1986) suggested that calanoids are limited in the Arctic by the inability to shorten their life cycle and reproduce within the short growing season. We detected few adult calanoids, and the copepodids tended to be associated with larger lakes, probably because they do not freeze to the bottom and can maintain populations throughout the winter. Thus, a change in the length of the growing season may improve the establishment success and persistence of calanoids and other slow-developing taxa in small Arctic lakes.

Overall, the lakes on Ellesmere Island show low microcrustacean species richness, diversity, and frequency of occurrence. Although the species pools around Lake Hazen and northern Ellesmere Island are similar, average species richness was greater around Lake Hazen. The low frequency of occurrence of species suggests that dispersal limitation is a key factor in structuring these microcrustacean communities. This was also supported by the low fraction of variation explained by spatial variables (7%) in the entire sample set on Ellesmere Island. Dispersal is more likely to be limiting in regions where there are large physical barriers to the movement of microcrustaceans and their vectors. Hessen et al. (2006) found evidence of dispersal limitation to isolated mountainous lakes in a 300+ lake survey in Norway, a landscape similar to that of the Arctic. In temperate systems, there is evidence of dispersal limitation when considering

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large geographic regions (Shurin et al. 2000); however, at small geographic and experimental scales, studies have found that dispersal is not limiting (Cottenie et al. 2003; Forrest and Arnott 2006).

Using variation partitioning, we observed large contributions of spatial and environmental variables to patterns in microcrustacean composition, especially in the Lake Hazen region. This is perhaps not surprising, as lakes in close proximity to each other would be more likely to influence species distributions via increased opportunity for short-distance dispersal events. Whiteside et al. (1980) found that recently formed moraine ponds in the Yukon had both calanoid and cyclopoid copepod species, as well as several cladoceran taxa, suggesting that a number of high latitude species can disperse quickly into new locales, in contrast to the view that passive dispersal in invertebrates is extremely limited (Bohonak and Jenkins 2003). Factors explaining microcrustacean community variation at different spatial scales and in different regions are generally consistent: spatial and environmental variables describe roughly equal fractions of variation, with the exception of the two larger scale studies (Québec and Ellesmere) where dispersal is more likely to be limiting at large spatial scales where long-distance dispersal events would be rare. Interestingly, fine-scale spatial variables were not important explanatory variables at either the small Lake Hazen region or the larger Ellesmere Island scale. This suggests that lakes that are very close together generally have similar communities, in agreement with the review of Havel and Shurin (2004), who suggested that dispersal could be rapid at distances <10 km, highlighting the importance of short-distance, frequent dispersal events. However, this may be species-specific: Hebert and Hann (1986) suggest that low dispersal rates have restricted the distribution of certain microcrustacean species, while Sarnelle and Knapp (2004) observed relatively rapid recolonization of lakes by *Daphnia middendorffiana* following removal of fish but failed to detect the copepod *Hesperodiaptomus shoshone*, which they attributed to significant Allee effects.

In contrast, broad and very broad scale spatial variables were important at both the Lake Hazen and Ellesmere Island scale, suggesting that there are likely some large barriers to dispersal that impede species from broadly colonizing the island. In the case of Ellesmere Island, the continuing retreat of the glaciers means that younger lakes, found closer to the glaciers, may show community compositions that exclude some of the slower dispersing species. In addition, younger lakes tend to have lower DOC concentrations and higher UV penetration, which likely will also affect species establishment and composition (Williamson et al. 2001). Finally, although we detected significant contributions of spatial and environmental variables to the total variation explained in microcrustacean community composition, a large portion of variation remained unexplained. This likely reflects our one-time sampling, which may have failed to capture important variation in environmental variables, as well as the entire microcrustacean community, which can be underestimated by 50% by single sampling visits (Arnott et al. 1998).

Local biotic factors are also an important determinant of microcrustacean species composition. We used nutrients as a proxy for phytoplankton productivity, as they represented a better measure of productivity than chl *a*, which has been shown to be poorly correlated with nutrients in Arctic lakes and ponds, where the predominant contributor is periphytic production (Keatley et al. 2007). Although the lakes in this study are generally fishless, there are other predators that may have an influence on the composition of microcrustaceans. Larger omnivorous copepods may have preyed on small-bodied microcrustaceans; however, these large predators were relatively rare in our study, as most assemblages were dominated by *D. middendorffiana/tenebrosa* or juvenile herbivorous stages of copepods. Other predator groups, such as waterbirds and larval insects, could also have influenced our results. For example, the migratory Red Phalarope waterbird (*Phalaropus fulicarius* (Linnaeus)), can consume *Daphnia*; however, predation rates are low at natural bird densities, suggesting that their impact is minimal (Dodson and Egger 1980). In addition, dipteran larvae were often found in microcrustacean samples, but their abundance was generally low.

Our survey revealed several species that had not been previously detected in lakes on Ellesmere Island. *Artemiopsis stefanssoni*, an anostracan, was identified on Ellesmere Island for the first time in this study. However, it is common throughout the Arctic, including northern Canada and eastern Greenland, and thus, Røen (1981) speculated that *A. stefanssoni* was present on Ellesmere in 1965 but that it was missed in his sampling. *Daphnia umbra* was first identified as a distinct species within the *D. longispina* complex by Taylor and Hebert (1994) and named by Taylor et al. (1996). Although there are records for this species in the lower Arctic, until now there were no records for *D. umbra* or *D. longispina* on Ellesmere Island. Similarly, *Tachidius discipes* has been recorded from other sites in the Arctic (Tash 1971) but not previously from Ellesmere Island. As a result of the scarcity of studies in this area, it is difficult to assess whether these species have recently dispersed to Ellesmere Island or whether they were simply not detected in previous studies. Experimental evidence has found that warming can reduce the invasion resistance of natural zooplankton communities (Holzapfel and Vinebrooke 2005), suggesting that a changing climate may facilitate species colonizations into new habitats. We hope that our study will provide important baseline information about microcrustacean communities against which future changes can be assessed.

Our study has found that the major controls on microcrustacean richness and community composition are factors that are closely related to climate. The Arctic is expected to be subjected to increased temperatures and precipitation in the coming decades (International Arctic Science Committee 2005). Warmer temperatures have altered both the biotic and abiotic characteristics of Arctic lakes. Decreased ice cover has led to longer growing seasons, which have been linked to greater productivity (Smol and Cumming 2000). Nutrients, DOC, and temperature were limiting factors in microcrustacean species distributions in our study, and the release of these constraints with increased warming could allow increased numbers of more southern species to colonize Ellesmere Island. Additionally, we demonstrated that High Arctic microcrustacean communities are structured differently than communities at lower latitudes: dispersal limits

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the ability of microcrustaceans to broadly colonize lakes and ponds on Ellesmere Island, while strong environmental gradients linked to climate change, i.e., high concentrations of DOC and nutrients flushed in from the watershed, are important determinants of survival and long-term persistence in the region.

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Yellow perch (*Perca flavescens*) stock structure in Lake Michigan: an analysis using mark–recapture data

David C. Glover, John M. Dettmers, David H. Wahl, and David F. Clapp

Abstract: To evaluate the stock structure of yellow perch (*Perca flavescens*) in the southern basin of Lake Michigan and in Green Bay, we analyzed recaptures from a lake-wide mark–recapture study implemented from 1996 to 2001 to infer the range and pattern of movement and spawning-site fidelity. Yellow perch generally moved south along the western shoreline, west along the southern shoreline, and north along the eastern shoreline during summer and non-summer months; the magnitude of movement was greater after spawning. Spawning yellow perch frequently returned to the same site, with 35%–80% of recaptured individuals returning to their marking site. Results from multiple tagging sites within Illinois indicated that spawners may return to larger areas rather than to specific sites, suggesting that large spawning complexes exist. Despite strong fidelity in some areas, straying was evident from all sites during spawning, resulting in mixing throughout the southern basin. Such mixing could promote gene flow and diminish stock differentiation. Dispersal of yellow perch within the southern basin of Lake Michigan occurred regularly across adjacent management boundaries. Therefore, adjacent jurisdictions may wish to consider re-examining their regulations based on this information to ensure consistent, complementary regulations that incorporate the movement patterns of yellow perch.

Résumé : Afin d'évaluer la structure du stock de perchaudes (*Perca flavescens*) dans le bassin sud du lac Michigan et dans Green Bay, nous avons analysé les recaptures provenant d'une étude de marquage et de recapture menée sur l'ensemble du lac en 1996–2001; nous en avons déduit l'étendue de la répartition et les patrons de déplacement, ainsi que la fidélité au site de fraye. Les perchaudes se déplacent généralement vers le sud le long de la rive ouest, vers l'ouest le long de la rive sud et vers le nord le long de la rive est durant les mois d'été et durant les autres mois; l'amplitude des déplacements est plus grande après la fraye. Les perchaudes en reproduction retournent souvent au même site de fraye, 35%–80% des individus recapturés étant retournés à leur site de marquage. Les résultats obtenus dans des sites multiples de marquage en Illinois indiquent que les reproducteurs peuvent retourner vers des endroits plus étendus que les sites spécifiques, ce qui laisse croire qu'il existe des complexes élargis de fraye. Malgré la forte fidélité à certains régions, il y a des indications d'errance dans tous les sites durant la fraye, ce qui cause des mélanges dans tout le bassin sud. Ce mélange pourrait favoriser le flux génique et réduire la différenciation des stocks. Il y a une dispersion régulière des perchaudes au sein du bassin sud entre les limites des différentes zones adjacentes de gestion. C'est pourquoi d'après ces renseignements, les administrations adjacentes pourraient vouloir réexaminer leurs règlements afin de s'assurer d'avoir des réglementations compatibles et complémentaires qui tiennent compte des déplacements des perchaudes.

[Traduit par la Rédaction]

Introduction

Stock identification and discrimination are fundamental issues in fisheries management that are used for a variety of purposes, including conservation of biodiversity, recovery of endangered species, the spatial allocation of harvest among competing fisheries, recognition and protection of critical spawning habitat, and development of optimal monitoring strategies (Waples 1995; Begg et al. 1999a; Stephenson 1999). Stocks are distinguished by differences in characteristics that could represent differing adaptations to variation in local environments, including life history and population parameters, morphometrics, meristics, physiology, behavior, calcified structures, and genetics (Ihssen et al. 1981; Pawson and Jennings 1996; Begg et al. 1999b). Divergence among these characters depends upon the degree of spatial and temporal isolation between stocks. Divergence is measured relative to the difference between the local environments that

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individual stocks experience (Ihssen et al. 1981; Pawson and Jennings 1996; Swain and Foote 1999). Disparities in these characteristics cause individual stocks to respond differently to exploitation. Therefore, stocks should be treated as separate biological units for management purposes (Ricker 1981; Gulland 1983; Stephenson 1999). Delineation of stocks has been recognized as a critical issue for management in the Great Lakes because of the decline of many ecologically and economically important fish species and the multijurisdictional challenges faced in these systems (Kutkuhn 1981).

Before 1997, yellow perch (*Perca flavescens*) was one of the most important, commercially fished species in Lake Michigan and contributed as much as 85% of the recreational harvest by number (Francis et al. 1996). However, estimated abundances of adult yellow perch in 2002 were approximately 8% and 20% of 1986 abundance in Wisconsin and Illinois, respectively (Wilberg et al. 2005). This reduction resulted partly from extremely poor recruitment since 1988 (Francis et al. 1996; Madenjian et al. 2002; Marsden and Robillard 2004) that was exacerbated by high fishing mortality and size-selective removal of larger fish (i.e., mature females; Heyer et al. 2001; Wilberg et al. 2005). Similar declines of yellow perch abundance occurred lake-wide, although declines were less drastic in Green Bay (Francis et al. 1996). Continued poor recruitment led to strict harvest regulations on the recreational fishery and a moratorium on commercial fishing in Lake Michigan (Francis et al. 1996; Marsden and Robillard 2004), although a limited commercial fishery remains active in Wisconsin waters of Green Bay (Clapp and Dettmers 2004), and a limited tribal commercial fishery is active in northeastern Lake Michigan. Predicting population responses to changes in fishing pressure is difficult, however, because the stock structure is poorly defined.

Determining whether multiple genetic stocks of yellow perch exist within Lake Michigan has proven difficult because of low levels of genetic variability observed with protein and mitochondrial DNA characters (Leary and Booke 1982; Billington 1996). Recent genetic research using hypervariable microsatellite DNA indicated that at least three genetically distinct groups of yellow perch exist in Lake Michigan: Green Bay, northern basin, and southern basin (Miller 2003). Yet, other work suggests that sympatric stocks may occur within these three genetic groups (Horns 2001). Length and condition of adult yellow perch along the western shoreline of southern Lake Michigan (i.e., Wisconsin and Illinois) were more similar to each other than to fish from Indiana and Michigan, suggesting an east–west spatial segregation within the population (Horns 2001).

Additional information about movement of yellow perch among areas of Lake Michigan would aid in managing this important fishery. Existing information relating to the movement of yellow perch in the Great Lakes is scarce, dated, and based on very few recaptures. A tagging study conducted in Green Bay indicated that most yellow perch were recaptured within 32 km of their release site, yet some individuals were recorded up to 81 km away (Mraz 1951). Similarly, 60% of all recaptured yellow perch released from Port Washington, Wisconsin, were recaptured within 16 km, with some straying up to 92 km (Smith and Van Oosten 1939). Tagging studies conducted in smaller systems also suggest that most yellow perch do not move far from their release location (Mansueti 1960; Fortin and Magnin 1972; Clady 1977) and demonstrate a high degree of site fidelity (Mansueti 1960; Muncy 1962; Aalto and Newsome 1990), which could provide a mechanism for spatial segregation. However, the movement of adult yellow perch has not been evaluated on a lake-wide scale in Lake Michigan. Strong site fidelity and limited movement by many individuals within Lake Michigan, coupled with a few rogue individuals traveling extreme distances, might maintain differences observed in population parameters in the southern basin of Lake Michigan (Horns 2001) but promote gene flow to reduce genetic variability over large areas (Slatkin 1987; Miller 2003).

Currently, yellow perch management units in the southern basin of Lake Michigan are delimited by state boundaries because the stock structure is poorly defined. Consequently, several stocks may be exploited within a state. Stocks that move across state lines or are located transboundary may be subjected to different fishing pressures. Thus, determining the movement of these putative stocks is imperative from a management perspective to facilitate the allocation of harvest among the four states that share the yellow perch fishery (Kutkuhn 1981; Horns 2001; Fu and Fanning 2004). We analyzed data from a mark–recapture study conducted from 1996 to 2001 in the southern basin of Lake Michigan and southern Green Bay to (*i*) describe the range and pattern of adult yellow perch movements and (*ii*) determine the extent to which yellow perch exhibit spawning-site fidelity. We used all information to determine the potential for the existence of sympatric stocks as well as evaluate current management boundaries.

Materials and methods

Yellow perch capture, marking, and recapture

Adult yellow perch were captured, marked, and released concurrently with annual assessments of spawning adults at nine locations in the southern basin of Lake Michigan and one location in the southern portion of Green Bay (Table 1; Fig. 1). Tagging was conducted during May and June from 1996 to 2000 in Illinois and from 1997 to 1999 in Indiana, Michigan, and Wisconsin waters. Yellow perch were tagged in Green Bay during April from 1997 to 1999. Tagging was conducted during the spring because yellow perch congregate in large numbers nearshore during spawning, making them more susceptible to capture.

Yellow perch were collected with a variety of gear types suitable for capturing fish >150 mm total length, including double-ended fyke nets, gill nets, and trap nets. All gear types were set in suitable habitat for capturing yellow perch during spawning and were retrieved within 24 h when possible. Rarely, unfavorable weather prevented their retrieval for up to 8 days (3 of 363 sets). The Illinois Natural History Survey (INHS) tagged fish at five sites in Illinois, including Waukegan Wiremill (IL-1), Lake Bluff (IL-2), North Lake Forest (IL-3), South Lake Forest (IL-4), and Fort Sheridan (IL-5; Table 1; Fig. 1). Yellow perch were captured at Mt. Baldy, Indiana (IN-1) by the Indiana Department of Natural Resources (INDNR) (Table 1; Fig. 1). Michigan Department of Natural Resources (MDNR) tagged fish at North St. Jo-

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Table 1. Location identifier, latitude (Lat.) and longitude (Long.) of each tagging location, years sampled, number of adult yellow perch (*Perca flavescens*) tagged, mean size (mm) at tagging with standard error (SE) in parentheses, and number of recaptures by source.

Location identifier	Tagging location (Lat., Long.)	Years sampled	No. tagged	Mean size (mm) at tagging (SE)	Recaptures		
					Agency	Sport	Commercial
GB-1	44°39.384′N, 87°59.571′W	1997–1999	7 198	171 (0.32)[b]	413	52	104
WI-1	42°59.035′N, 87°50.250′W	1997–1999	9 615	239 (0.23)[e]	543	53	0
IL-1	42°20.244′N, 87°49.462′W	1997–2000	4 633	244 (0.46)[e]	410	59	0
IL-2	42°16.772′N, 87°49.502′W	1996	4 210	231 (0.38)[d]	424	124	57
IL-3	42°15.280′N, 87°49.015′W	1996–2000	11 167	241 (0.27)[b]	658	83	35
IL-4	42°13.950′N, 87°48.435′W	1997–1999	1 766	238 (0.63)[e]	123	25	9
IL-5	42°12.789′N, 87°47.792′W	1996–2000	10 952	240 (0.28)[b]	522	142	75
IN-1	41°42.912′N, 86°56.095′W	1997–1999	6 410	185 (0.41)[g]	233	115	0
MI-1	42°8.166′N, 86°28.454′W	1997–1999	5 240	217 (0.45)[f]	312	187	0
MI-2	42°6.154′N, 86°30.200′W	1997–1999	2 757	216 (0.59)[f]	163	104	0
Total			63 948		3 801	944	280

Note: Recaptures are from 1996 to 2001 for Illinois tagging locations and from 1997 to 2001 for all other locations. Mean sizes at tagging with similar letters did not significantly differ ($\alpha = 0.05$).

seph (MI-1) and South St. Joseph (MI-2; Table 1; Fig. 1). Wisconsin Department of Natural Resources (WDNR) captured and tagged fish at Green Can Reef (WI-1), as well as at Little Tail Point (GB-1; Table 1; Fig. 1).

All yellow perch were measured (nearest mm, total length), and sex was determined by discharge of milt or eggs. Fish over 150 mm (120 mm in Green Bay) and in good condition were tagged and immediately released. Individually numbered Floy FD-94 anchor tags were inserted on the left side, above the lateral line and below the soft rays of the dorsal fin. The INHS address and phone number was also imprinted on all tags to facilitate returns.

Tagged fish were recaptured by commercial fishermen, recreational anglers, and state fisheries agencies from 1996 to 2001. The tag number, date, recapture location, sex, and total length (nearest mm) were recorded for each yellow perch recaptured. For yellow perch recaptured by commercial and recreational sources, information was requested for the tag number, date, and location. Details about the project and information specific to the recaptured yellow perch (e.g., length, sex, date, and location tagged) were sent to anglers that supplied contact information. Occasionally, inconsistencies were found with a reported tag recaptured by recreational anglers (e.g., INHS zip code reported as tag number). Unless inconsistencies could be verified with the original tag, these recaptures were omitted from analyses.

Data analysis

To describe the range and pattern of adult yellow perch movements, the spatial distribution of sport recaptures was analyzed from each release site. Sport recaptures were used because they exhibited greater spatial and temporal variation than agency recaptures. The ban on commercial fishing in Lake Michigan proper during most of the tagging study limited the utility of commercial recaptures for movement analyses. However, all sources of recapture were used later in spawning-site fidelity analyses.

Data standardization

To account for spatially disproportionate angling effort that can bias movement analyses (Hilborn 1990), estimates of directed angler effort (h) for yellow perch were incorporated. Annual creel surveys were conducted for each port or county within each state. Monthly estimates of harvest were pooled by Lake Michigan management units for each species by fishery type (i.e., boat, charter, shore, and stream anglers). Specific information regarding the estimation of angler effort can be obtained from creel surveys conducted within Wisconsin (Peterson and Eggold 2003), Illinois (Brofka and Dettmers 2004), Indiana (Palla 2003), and Michigan (Lockwood 1999; Lockwood et al. 1999). To account for spatial differences in angler effort at the smallest scale possible, we obtained these estimates separated by port for Illinois (W. Brofka, INHS, Lake Michigan Biological Station, 400 17th Street, Zion, IL 60099, USA, unpublished data), Indiana (J. Palla, INDNR, Lake Michigan Fisheries Office, 100 W. Water Street, Michigan City, IN 46360, USA, unpublished data), and Michigan waters (D. Clapp, MDNR, Charlevoix Fisheries Research Station, 96 Grant Street, Charlevoix, MI 49720, USA, unpublished data) and by county for Wisconsin waters (B. Eggold, WDNR, 600 East Greenfield Avenue, Milwaukee, WI 53204, USA, unpublished data) for each year of the tagging study (1996–2001; Fig. 1). Michigan did not separate effort directed at a specific species until 1997. To obtain angling effort directed at yellow perch during 1996 in Michigan waters, the ratio between effort directed at yellow perch and effort directed at all species for 1997 to 2001 (0.14) was multiplied by the effort directed at all species in 1996. Creel surveys were conducted in Wisconsin from March to October (March–April and September–October were combined into two single estimates), but no county was consistently surveyed during March and April throughout the tagging study. All ports in Illinois were surveyed from April to September each year. Ports in Indiana and Michigan were sampled from April to October, with the exception of St. Jo-

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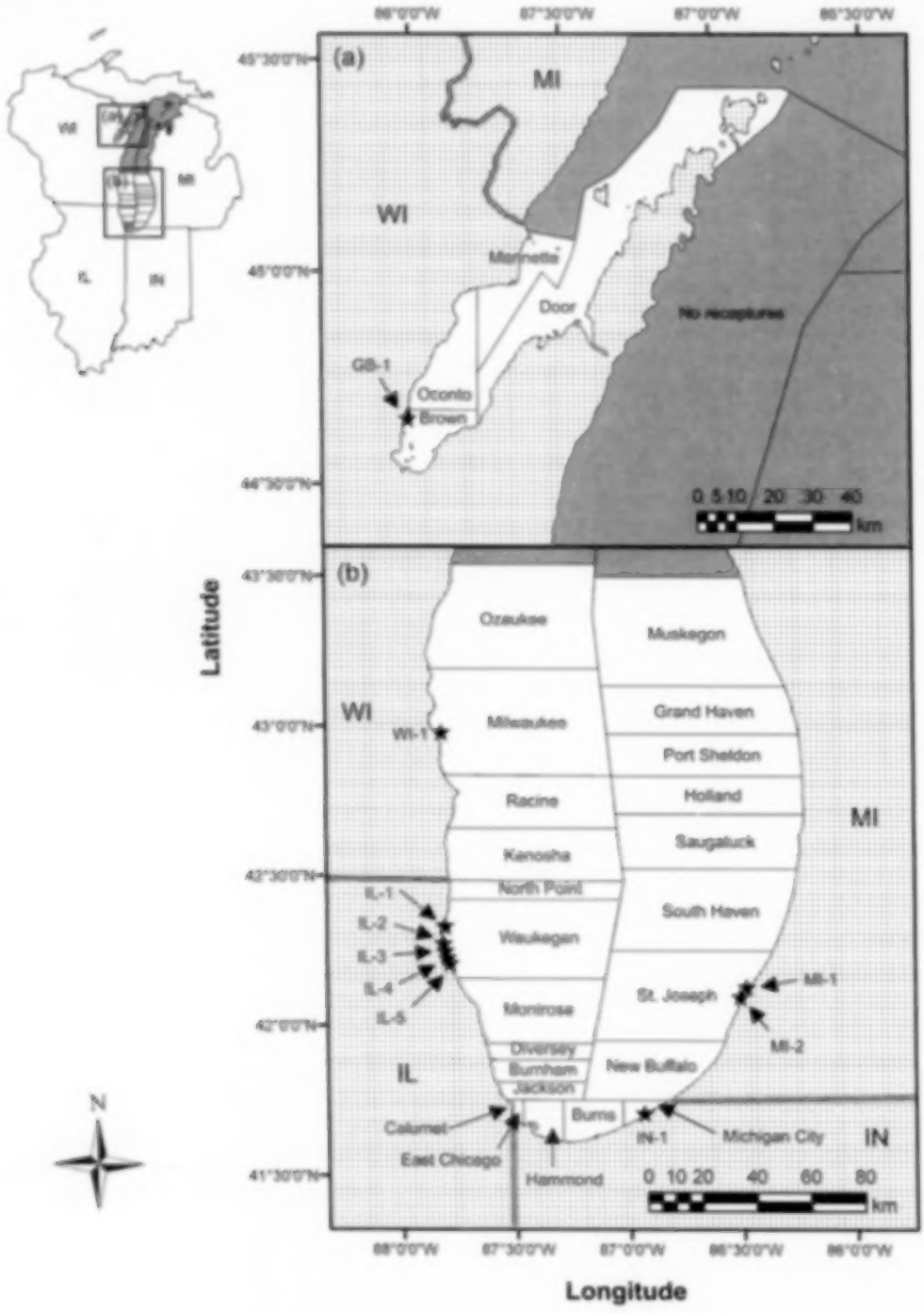
Fig. 1. Map of Lake Michigan with inset sections of Green Bay (*a*) and southern Lake Michigan (*b*), tagging sites (stars), and creel survey sampling areas. Creel units for each port were derived by drawing straight lines from the midpoint between ports to their respective state line. Existing county lines were used to delineate creel units in Wisconsin waters of Lake Michigan and Green Bay. No recaptures occurred in the gray-shaded waters.



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seph, Michigan, and New Buffalo, Michigan, which were also sampled in March. For analyses concerning fish released in Illinois, angler effort was summed across 1996 to 2001 into two recapture periods: summer (June–August) and non-summer (March–May and September–October). Additionally, angler effort was summed across both recapture periods (March–October) when there were too few recaptures during the non-summer recapture period to provide a depiction of overall movement across the study period. For all other areas, angler effort was summed from 1997 to 2001 into the same recapture periods because tagging commenced 1 year after tagging began in Illinois. Rare recaptures that occurred from November through February were omitted because no estimates of angler effort directed at yellow perch were available.

Each recaptured yellow perch was assigned the amount of estimated angler effort from the creel unit in which it was recaptured. Creel units for each port were derived by drawing straight lines from the midpoint between ports to their respective state boundary within the lake. Existing county lines were extended into the lake to delineate creel units in Wisconsin waters of Lake Michigan and Green Bay. Distance moved was calculated as the straight-line distance from the tagging location to the closest possible location of reported recapture (e.g., street names of cities and towns, harbors, piers, beaches, power plants, water filtration plants). To determine the direction moved, we assigned directional movement for each fish as follows: north (315°–45°), south (135°–225°), east (45°–135°), or west (225°–315°). Fish recaptured at the original tagging location were omitted from the directional analyses to reduce the potential of underestimating mean movement in a particular direction. Fish that moved toward the shoreline from recapture sites (i.e., in small creeks or harbors) were assumed to represent no movement and were also omitted. These scenarios were extremely rare for sport recaptures and did not change the interpretation of the results.

Dispersal distance

Dispersal distance, which we defined as the distance within which 90% of the recaptures per effort (RPE) occurred (Schmalz et al. 2002), was used as an index of home range for a group of individuals. The RPE for each recapture location was calculated as the number of recaptures per 10 000 angler hours directed at yellow perch. We assumed that angler effort was uniformly distributed within each port and county, which allowed us to assign several recapture locations within each area with identical estimates of angler effort. We feel that this is a reasonable assumption given the resolution of angler effort we were able to obtain. The cumulative proportion of RPE (y) was fit to an exponential sigmoid function of distance from each tagging location:

$$(1) \qquad y = \frac{\alpha}{\left(1 + \beta\, e^{Kx}\right)}$$

where α is the maximum cumulative proportion of RPE that can be obtained (theoretically 1.0 or 100%), β is a parameter that scales the function toward zero, and K is the rate at which RPE increases with distance (x). The modified Gauss–Newton iterative method that relies on exact derivatives was used to determine the parameters that produce the lowest residual sum of squares for each tagging location (PROC NLIN; SAS Institute Inc. 1999). Using derived parameters, the distance (x) at which the cumulative proportion of RPE (y) was equal to 0.90 (90%) was estimated for each tagging location and recapture period. We applied this analysis to recaptures during summer and to total time periods (summer and non-summer time periods combined). Although the summer and total time periods are not independent, insufficient recaptures occurred during the non-summer period to allow numerical convergence when considered alone. Therefore, it was necessary to estimate dispersal during the total time period to provide information about the range of non-summer movement that would otherwise not be displayed.

ArcView, version 3.2 (Environmental Systems Research Institute 1998) was used to develop a linear scale for shoreline distance in the southern basin of Lake Michigan to assess dispersal across management boundaries and overlap among fish released from the various tagging locations (shoreline data provided by E. Marshall, University of Michigan, Institute for Fisheries Research, 1109 North University Street, Museum Annex Building, Ann Arbor, MI 48103, USA). Shoreline distance was used because all recaptures occurred nearshore throughout the study except in Green Bay. The shoreline distance scale began at the northern border of Ozaukee County, Wisconsin (43°32.528′N, 87°47.607′W; Fig. 1) and continued counterclockwise around the southern basin, ending at the northern border of the Muskegon creel unit, Michigan (43°30.233′N, 86°26.714′W; Fig. 1). Dispersal was expressed in terms of shoreline distance by creating 90% dispersal buffers around each tagging location for each recapture period and determining the point at which the buffer crossed the shoreline. All recaptures, tagging sites, and management boundaries were similarly translated into shoreline distance.

Directional movement

To describe directional movement of adult yellow perch, we used separate weighted analyses of variance (ANOVA; PROC MIXED; SAS Institute Inc. 1999) for each major tagging area (i.e., Green Bay, Wisconsin, Illinois, Indiana, and Michigan). We examined the effect of tagging sites (T), recapture periods (R; summer and non-summer), the interaction between tagging sites and recapture periods (TR), direction nested within recapture periods ($D(R)$), and the interaction between tagging sites and distance nested within recapture periods ($TD(R)$) on mean movement. Time-at-liberty (L) was also included to test whether the variance of movement distance increased with time. To correct for disproportionate angler effort, each recaptured yellow perch was weighted by the reciprocal of the appropriate angler effort (h). We did not include the effect of T and its interactions for models that had only one tagging location (i.e., Green Bay, Wisconsin, and Indiana). To evaluate whether similar trends occurred at closely spaced tagging locations, T was included in the Illinois and Michigan models. Directions in which few recaptures (three or less) occurred in the specific recapture period were omitted from the analysis. Residuals were assessed for normality.

If F tests were significant at $\alpha = 0.05$, we minimized the type I experiment-wise error using post hoc one-tailed t tests

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at the $\alpha = 0.025$ level to determine whether (*i*) there was directional preference from each tagging location by determining whether the largest directional mean distance traveled was statistically larger than the distance traveled in all other directions, (*ii*) the magnitude of directional movement was greater in summer as compared with non-summer periods when the preferred direction of movement was similar between periods, and (*iii*) mean movement was greater during the non-summer recapture period.

Fidelity and movement

We used separate baseline-category logit models for each tagging site to determine the probability of fish being recaptured at their release site as well as the probability of being recaptured at other sites or areas for the entire study. Probabilities were transformed from odds ratio estimates calculated using maximum likelihood procedures (PROC LOGISTIC; SAS Institute Inc. 1999) and were then converted to percentages by multiplying by 100. Analysis of recaptures was limited to spawning seasons (May–July in Lake Michigan; April–June in Green Bay) at least 1 year after tagging. Estimating the probability of movement to areas other than the tagging site allowed us to determine (*i*) whether fidelity occurred at a larger scale (i.e., nearby tagging locations within the same region), (*ii*) if some areas represented transition zones in which fish were caught en route to more preferred spawning areas, and (*iii*) the percentage of fish moving across jurisdictional boundaries. Wald χ^2 statistics were used to test whether the observed probability of fish being caught at the tagging site was greater than that observed at other locations. In Illinois, IL-2 and IL-4 were excluded from the fidelity analysis, because no or low effort was expended to recapture yellow perch at these sites after initial tagging. Rather than omitting fish recaptured at IL-2 and IL-4 that were released from other sites, they were pooled into our analysis of all Illinois waters (IL).

Results

Yellow perch capture, marking, and recapture

Throughout the study, 63948 adult yellow perch were tagged (Table 1). The mean size at tagging ranged from 171 to 244 mm and differed among tagging sites ($F_{[9, 63807]} = 5578.45$; $P < 0.001$; Table 1). Sometimes disparities in size at tagging among tagging sites may represent biologically meaningful differences (e.g., fish tagged at Green Bay were smaller than fish tagged in the open lake). However, large sample sizes increased the power to detect small differences among locations and may not always represent biologically meaningful differences (e.g., between MI-1 and MI-2). The sex ratio of tagged individuals was highly skewed toward males (18:1), and only about 4% of all tagged individuals could not be sexed. A total of 5025 yellow perch were recaptured between 1996 and 2001 (Table 1), which represented an overall recapture rate of 7.9%. Agency, sport, and commercial returns accounted for 75.6%, 18.8%, and 5.6% of all recaptures, respectively. Mean time-at-liberty was 224 days and ranged from 0 to 2004 days (5.5 years), with 92% of all recaptures occurring within 2 years of release.

Dispersal distance

The proportion of total variability explained (R^2) by the dispersal distance models ranged from 0.94 to 0.99, indicating that describing the cumulative proportion of RPE as an exponential sigmoid function of distance fit the data very well for both summer and total recapture periods. During summer, 90% dispersal distance from GB-1 was 28.7 km, which remained within the Wisconsin waters of Green Bay. In the southern basin, dispersal distance averaged 60.4 km (all sites combined) but was quite variable among sites, ranging from 12.8 to 101.4 km. Ninety percent of the recaptures from WI-1 occurred within the Wisconsin waters of Lake Michigan. However, dispersal distances from four out of five Illinois tagging sites crossed the Illinois border into Wisconsin waters. The 90% dispersal distance from IL-3 also crossed into Indiana waters. For the fish released at site IN-1, 90% of the recaptures were reported within 44.3 km, resulting in overlap into Michigan waters. Dispersal from MI-2 crossed into Indiana waters, whereas dispersal from MI-1 extended 101.4 km, well into Illinois waters.

Considerable amounts of mixing by tagged fish within and among jurisdictions occurred during summer (Fig. 2). Dispersers from Illinois and Michigan waters overlapped considerably among nearby sites, many being completely within the dispersal area of another site, indicating little potential for isolation by distance within states (Fig. 2). Mixing among states occurred between adjacent states, with the exception of Michigan and Illinois.

Dispersal distances for the total recapture period exceeded those of summer for all sites except for fish from IL-3 and MI-1. Dispersal distance could not be estimated for IL-1 and MI-2 because the estimated maximum cumulative proportion of RPE (α) was below 0.90, likely because too few recaptures occurred far from the release site. Although the dispersal distance increased when considering the entire time period, movement from GB-1 and WI-1 remained within the local management jurisdiction. Dispersal from four sites in Illinois waters crossed into Wisconsin waters (Fig. 2). Dispersal from two sites in Illinois crossed into Indiana waters. Ninety percent of the fish from IN-1 were recaptured within 58.8 km, resulting in movement into both Illinois and Michigan waters. Dispersal from MI-1 extended 80.5 km, crossing into Indiana waters.

Mixing among dispersers during the total time period was limited to mixing among fish released from adjacent states (Fig. 2). However, as a result of increased dispersal distances during the total time period, the mixing that occurred between Illinois and Wisconsin and between Illinois and Indiana increased slightly compared with summer. Dispersal among all sites within Illinois was completely overlapped.

Directional movement

Time-at-liberty affected the variability of distance traveled from Illinois, Indiana, and Michigan tagging areas but not from Green Bay or Wisconsin (Table 2). Thus, we omitted this term from the Wisconsin and Green Bay models. Recapture period affected the mean distance traveled for all tagging areas except Green Bay (Table 2). Specifically, non-summer movement was greater than summer movement in Illinois, Indiana, and Michigan waters ($t \geq 6.30$, $P < 0.001$),

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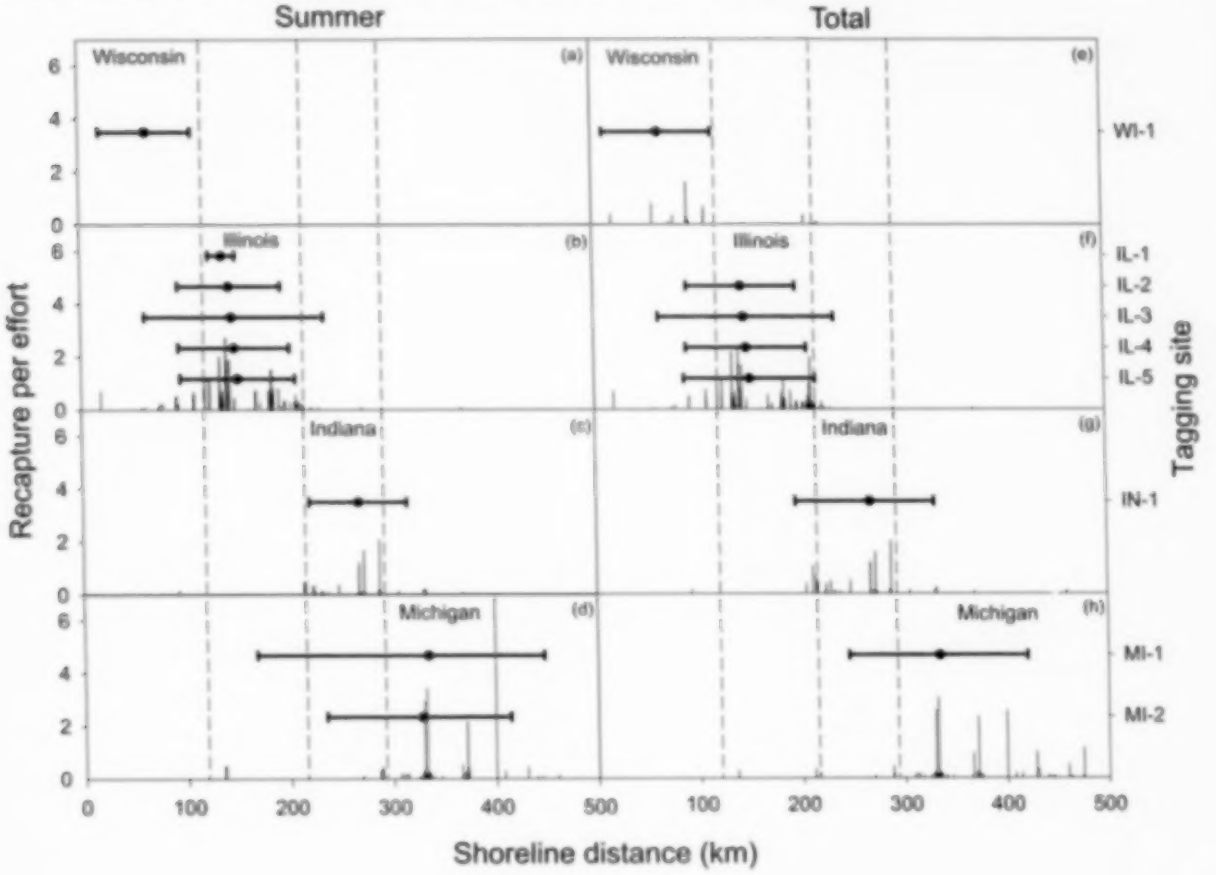
Fig. 2. Number of recaptures per effort (vertical bars) during the summer and total time periods at specific locations expressed as shoreline distance (km) for yellow perch (*Perca flavescens*) released from Wisconsin (*a* and *e*), Illinois (*b* and *f*), Indiana (*c* and *g*), and Michigan (*d* and *h*). Tagging sites are indicated with solid circles; 90% dispersal distance from each tagging site is shown by horizontal bars and is expressed in shoreline distance rather than straight-line distance (i.e., the point at which the 90% straight-line buffer transected the shoreline). The shoreline distance scale begins at the northern border of Ozaukee County, Wisconsin, and continues counterclockwise around the southern basin, ending approximately at the northern border of the Muskegon Fishery creel unit, Michigan, and corresponding to the unshaded portion of Fig. 1*b*. Vertical broken lines represent the point on the scale at which state boundaries occur.



but less than summer movement for fish released from Wisconsin waters ($t = 4.12$, df = 44, $P < 0.001$).

Directional preference by yellow perch was evident at all tagging sites in at least one recapture period, as the direction within recapture period was significant for Green Bay, Wisconsin, and Indiana waters, and an interaction with tagging sites was observed for returns from Illinois and Michigan sites (Table 2). During summer months, yellow perch traveled farther south than north from WI-1, IL-2, IL-3, IL-4, and IL-5 (Table 3). Fish from IN-1 and MI-1 moved at greater distances westward and northward, respectively, than any other direction observed from these sites during the summer (Table 3).

During non-summer months, yellow perch traveled farther east than south from GB-1 (Table 3). The distance traveled southward was greater than northward for all Illinois sites during the non-summer recapture period (Table 3). The magnitude of southward movement increased during non-summer months compared with summer months for IL-2 ($t = 5.67$, df = 399, $P < 0.001$), IL-3 ($t = 2.25$, df = 399, $P = 0.01$), and IL-5 ($t = 4.60$, df = 399, $P < 0.01$). During non-summer months, yellow perch only moved westward from IN-1 (Table 3) for greater distances compared with summer ($t = 2.28$, df = 82, $P = 0.01$). Only northward movement from MI-1 and MI-2 was observed during the non-summer recapture period (Table 3). This movement northward was greater during non-summer months when compared with summer ($t = 5.21$, df = 268, $P < 0.001$).

Fidelity and movement

The percentage of yellow perch recaptured in at least one spawning season after release was greatest at the site of release for GB-1 ($\chi^2_1 = 4.61$, $P = 0.03$), WI-1 ($\chi^2_1 > 13.46$, $P < 0.001$), IL-1 ($\chi^2_1 > 26.76$, $P < 0.001$), IL-3 ($\chi^2_1 > 26.82$, $P < 0.001$), and IN-1 ($\chi^2_1 > 7.25$, $P < 0.01$) (Fig. 3). Fish released from IL-5 showed higher fidelity for the release site

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Table 2. Analysis of variance results for directional preference for each tagging area, comparing movement distance between recapture periods (*R*; summer, non-summer), direction nested within recapture periods (*D*(*R*)), tagging sites (*T*), tagging sites between recapture periods (*TR*), and the interaction between tagging sites and distance nested within recapture periods (*TD*(*R*)).

	Green Bay			Wisconsin			Illinois			Indiana			Michigan		
Factor	*F*	df	*P*	*F*	df	*P*	*F*	df	*P*	*F*	df	*P*	*F*	df	*P*
L	0.64	1, 40	0.43	1.36	1, 43	0.25	28.4	1, 399	<0.001	7.69	1, 82	0.01	20.62	1, 268	<0.001
R	0.87	1, 41*	0.36	16.96	1, 44*	<0.001	39.63	1, 399	<0.001	161.68	1, 82	<0.001	53.29	1, 268	<0.001
D(*R*)	11.01	3, 41*	<0.001	5.33	1, 44*	0.03	68.78	2, 399	<0.001	34.72	2, 82	<0.001	8.99	1, 268	<0.01
T	—	—	—	—	—	—	5.06	4, 399	<0.001	—	—	—	3.82	1, 268	0.05
TR	—	—	—	—	—	—	6.51	4, 399	<0.001	—	—	—	3.94	1, 268	0.05
TD(*R*)	—	—	—	—	—	—	3.69	8, 399	<0.001	—	—	—	9.67	1, 268	<0.01

Note: Time-at-liberty (*L*) tested whether the variance of movement distance increased with time. The effect of tagging location and its interactions was tested at Illinois and Michigan only because these areas contained multiple tagging sites.

*These statistical results were determined after the removal of the insignificant time-at-liberty (*L*) term from the directional preference model.

Table 3. Mean distance traveled (km) by yellow perch (*Perca flavescens*) determined from sport recaptures, adjusted by directed angler effort (h) for yellow perch in each direction relative to the tagging location (standard error, SE, in parentheses) during summer and non-summer recapture periods.

	Distance moved relative to tagging location			
Location identifier	North	South	East	West
Summer				
GB-1	12.6 (2.7)	5.0 (4.5)	11.6 (3.4)	—
WI-1	20.5 (4.2)	31.3 (2.1)*	—	—
IL-1	10.7 (3.0)	11.4 (3.2)	—	—
IL-2	10.9 (2.1)	28.7 (2.7)*	—	—
IL-3	19.1 (3.4)	39.6 (4.3)*	—	—
IL-4	22.7 (4.4)	44.2 (5.9)*	—	—
IL-5	24.4 (2.4)	35.1 (2.4)*	—	—
IN-1	—	1.1 (4.5)	9.1 (2.2)	40.5 (3.5)*
MI-1	38.8 (4.5)*	1.0 (5.0)	—	—
MI-2	18.3 (5.1)	19.1 (10.0)	—	—
Non-summer				
GB-1	—	3.9 (2.3)	20.2 (1.9)*	—
WI-1	6.0 (4.2)	—	—	—
IL-1	23.2 (8.6)	64.6 (4.1)*	—	—
IL-2	11.6 (3.0)	55.2 (3.9)*	—	—
IL-3	33.9 (8.6)	50.6 (2.5)*	—	—
IL-4	12.5 (4.1)	51.2 (4.8)*	—	—
IL-5	27.1 (4.2)	50.0 (1.9)*	—	—
IN-1	—	—	—	49.0 (1.8)
MI-1	62.1 (6.6)	—	—	—
MI-2	43.3 (6.6)	—	—	—

Note: An asterisk (*) represents the preferred direction from a site (α = 0.025). A dash (—) indicates that no yellow perch were recaptured in that respective direction.

compared with all other recapture locations ($\chi^2_1 > 23.21$, $P < 0.001$), with the exception of IL-3 ($\chi^2_1 = 1.47$; $P = 0.27$). Fish released from MI-1 were 8.3 times more likely to be recaptured at their release site than at MI-2 ($\chi^2_1 = 39.97$, $P < 0.001$), but were only slightly less likely to be caught anywhere within Michigan waters ($\chi^2_1 = 2.72$, $P = 0.10$). Fish recaptured from MI-2 did not display greater fidelity to any area within Michigan ($\chi^2_1 < 1.32$, $P > 0.31$; Fig. 3). Although the majority of recaptures occurred at nearby sites within the state released, some yellow perch ventured across adjacent state lines (i.e., WI-1, IL-1, and MI-2) and even multiple state lines (i.e., IL-3, IL-5, IN-1, MI-1, and MI-2) (Fig. 3).

Discussion

In the southern basin of Lake Michigan, tagged adult yellow perch generally moved south along the west side of the lake, west along the south side of the lake, and north along the east side of the lake. Movement direction was largely consistent across time periods. The magnitude of these movements was typically small during summer, ranging between 13 and 101 km, but increased during non-summer months. In addition, the proportion of yellow perch returning to the identical or nearby locations in subsequent spawn-

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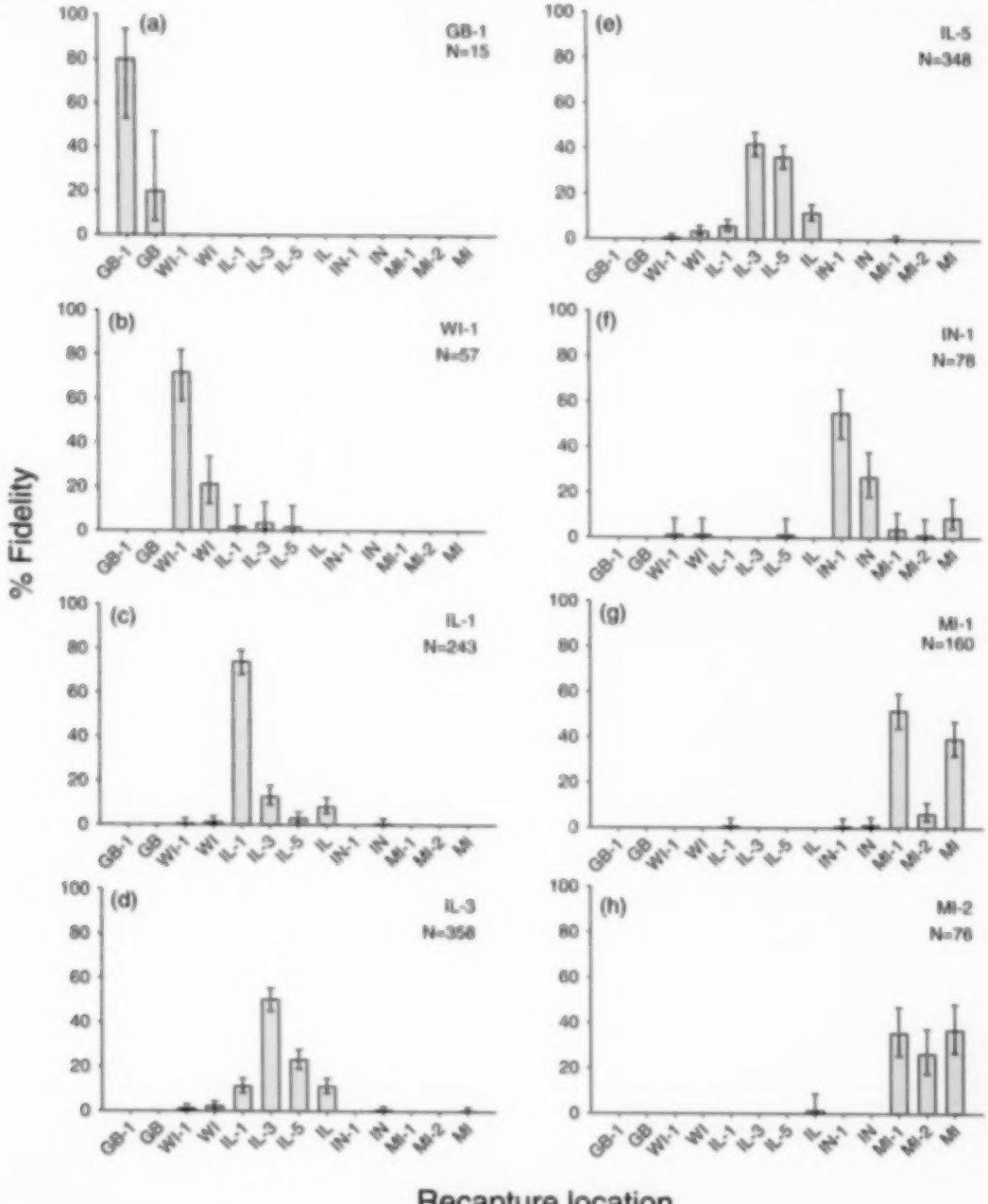
Fig. 3. Percentage of tagged yellow perch (*Perca flavescens*) from each tagging site ((*a*) GB-1, (*b*) WI-1, (*c*) IL-1, (*d*) IL-3, (*e*) IL-5, (*f*) IN-1, (*g*) MI-1, (*h*) MI-2) that were recaptured at various locations during subsequent spawning seasons. Error bars represent the 95% confidence intervals. *N* is the total number of recaptures that occurred during spawning seasons subsequent to tagging, which include agency, sport, and commercial sources.



ing seasons was high (35%–80%), particularly along the west shoreline of southern Lake Michigan and in Wisconsin waters of Green Bay. Yet, fish released from Illinois were recaptured at all other sites within Illinois, suggesting that yellow perch in these waters were not faithful to an exact spawning location, but remained faithful to a much larger area. This contrasts with studies in much smaller systems such as Long Lake, Michigan, where homing by displaced yellow perch to an exact location was documented (Hodgson et al. 1998). Nevertheless, faithfulness to certain spawning

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areas throughout the southern basin of Lake Michigan could provide a mechanism to isolate groups of yellow perch for the formation of sympatric stocks.

Despite high fidelity to certain sites, straying occurred from all sites, resulting in mixing among all areas in the southern basin except between Michigan and Wisconsin waters. Further, no fish tagged in the southern basin were caught within the northern basin. Because this straying occurred during spawning seasons, it increases the chance for gene flow among areas (Slatkin 1987), supporting the conclusion that a homogenous genetic population exists within the southern basin (Miller 2003). In addition, our results are based on nearshore recaptures of adult yellow perch. Therefore, the estimated mixing within the southern basin is conservative considering that any potential offshore movement and mixing is underrepresented in this study. These results demonstrate that movement of adult yellow perch can contribute to the genetic homogeneity within the southern basin, whereas Miller (2003) speculated the homogeneity to be mainly from larval mixing via ocean-like currents (Beletsky et al. 1999). Also, a single yellow perch from Fort Sheridan, Illinois, was recaptured in Green Bay, which we considered an outlier in both directional and dispersal models. This type of large-scale movement by a few individuals can contribute to low genetic variability within Lake Michigan.

Offshore advection of larval yellow perch via wind-induced currents (Dettmers et al. 2005), combined with counterclockwise, ocean-like gyres (Beletsky et al. 1999), likely transfers larval fish large distances within each basin, further decreasing the likelihood of genetic differentiation. The transfer of a single dispersing age-0 fish per generation has the potential to diminish the effects of local adaptation and maintain basin-wide genetic homogeneity (Slatkin 1987; Taylor 2003). Characteristics of smaller systems than Lake Michigan may increase the potential for larval retention within spawning areas, increasing the probability of forming sympatric stocks (e.g., Aalto and Newsome 1993). In Lochaber Lake, Nova Scotia, Canada, indirect evidence suggested that larval yellow perch became acquainted with the spawning area to allow later homing (Aalto and Newsome 1990). Mixing at both the larval and adult life stages within the southern basin of Lake Michigan therefore decreases the likelihood of sympatric yellow perch stock formation.

Although we could not directly associate patterns of movement with habitat characteristics, our data suggest interesting relationships that deserve further investigation. Previous work has indicated that substrate type and availability is important to the spawning and feeding of yellow perch in Lake Michigan. Yellow perch select cobble substrate for spawning in Lake Michigan (Robillard and Marsden 2001), but also select these areas during other time periods because preferred prey, such as crayfish, sculpins (*Cottus* spp.), and alewife (*Alosa pseudoharengus*) (Powers and Robertson 1968; Janssen and Quinn 1985; Janssen and Luebke 2004) typically favor rocky habitat. Abundant zebra mussels (*Dreissena polymorpha*) in rocky areas of Lake Michigan (Fleischer et al. 2001) also increase abundance of other invertebrates important in the diet of yellow perch (Stewart et al. 1998; Kuhns and Berg 1999; Cobb and Watzin 2002). Further investigation may therefore be warranted to determine the role of substrate type and availability in regulating movement of individual yellow perch and the structure of the population.

Our estimates of dispersal distance and direction were based on an accepted technique to estimate movements of fish that corrects for nonuniform distribution of spatial and temporal fishing effort (Schmalz et al. 2002). Complete removal of bias from spatially disproportionate effort may be impossible, but this technique offers the best available tool to remove bias. Differences in harvest policies among states, particularly bag limits, are considered reflected in the angling effort that was estimated from the creel surveys; as a result, these differences should be accounted for using this data standardization technique. Only the size distribution of yellow perch being harvested should be affected, not the size of yellow perch caught by anglers. Thus, size limits impose a bias only if they affect the reporting rate of anglers. During our study, a size limit to keep 200–250 mm yellow perch was in effect only in Illinois waters. The number of recaptures from Illinois waters was sufficiently high to indicate that the slot limit did not appreciably affect tag reporting rate.

Dispersal of yellow perch within the southern basin of Lake Michigan always crossed management boundaries (particularly between adjacent states). The summer movement period includes spawning, during which many males tend to linger in spawning areas (Muncy 1958). Because the population was largely skewed toward males at the time of tagging, this may have increased the probability of recovering fish close to spawning areas. Additionally, our models of dispersal distance indicated that only fish from Green Bay and Wisconsin waters stayed within local management boundaries during both time periods. However, yellow perch exhibited directional preference during summer and nonsummer time periods. Although fish from four of five Illinois sites moved into Wisconsin waters during summer, the preferred directional movement was southward from these sites during this time period, thus decreasing the number of fish likely crossing into Wisconsin as well as the amount of mixing with fish in Wisconsin waters. This argument could be extended to dispersal during total recapture periods when directional preference was similar between the two recapture periods (e.g., Illinois, Indiana, and Michigan), increasing the likelihood of mixing between fish from Illinois and Indiana waters, but decreasing the likelihood of mixing between fish from Indiana and Michigan waters. Therefore, both dispersal distance and directional preference should be considered when evaluating movement of yellow perch.

Horns (2001) documented similarities in length and condition of adults and their size at age-1 between fish from Wisconsin and Illinois waters. Fish from Indiana waters were greater in size at age-1 than fish from all other areas, but were smaller and in poorer condition compared with adults. His results suggested a separation for management between Indiana and Illinois–Wisconsin. However, our results suggest that mixing is strong among fish from Wisconsin, Illinois, and Indiana waters, suggesting that fish in Indiana waters were not a separate stock. Yet, our results do suggest that fish from Michigan waters may be spatially segregated because they tend to move away from fish released in waters of the other three states. While our results support

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the assignment of a single genetic stock within the southern basin of Lake Michigan, environmentally induced phenotypic expressions of local environments will still cause groups to respond differently to exploitation (Pawson and Jennings 1996; Swain and Foote 1999). Therefore, managers should carefully consider the delineation of biologically significant management boundaries that not only encompass the directed range of yellow perch movements, but also consider differences in population characteristics such as growth rates. Further, most tagged yellow perch remained within their respective management unit, indicating the current delineation of management units is reasonable. Nevertheless, because movement occurred across management boundaries between adjacent states based on these nearshore recaptures, we recommend that adjacent states consider re-examining their regulations based on this information to ensure consistent, complementary regulations that incorporate the movement patterns of yellow perch.

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A diver survey design to estimate absolute density, biomass, and spatial distribution of abalone

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Abstract: Abalone surveys worldwide measure relative stock abundance. However, important advantages accrue if diver surveys measure absolute numbers or biomass per square metre. Principally, absolute biomass permits quota setting from a single survey using a decision table. Although relative abundance surveys have permanently fixed sampling protocols and locations, absolute abundance survey designs can be improved with technology over time. Furthermore, surveys can be directed to areas of principal management focus, and absolute survey population numbers by length with confidence intervals provide informative model input. We propose and test a transect survey design to estimate and map absolute density and biomass of abalone or other sedentary invertebrates. Divers count and measure all abalone within 1 m of a 100 m, boat-deployed leaded rope line. Semi-systematic transect locations provide spatially representative sampling inside bounded survey regions and geostatistical data for contour maps of abalone density and mean size. The effectiveness of the design for estimating change in population size under harvesting and for locating areas of fishable density was tested by a fish-down experiment, using surveys run before and after commercial harvest. The leaded-line survey design estimates of population change and spatial distribution showed agreement with the fish-down experimental harvest.

Résumé : Les inventaires d'ormeaux partout dans le monde mesurent l'abondance relative des stocks. Cependant, ce serait un avantage additionnel de faire en plongée des inventaires des nombres ou de la biomasse absolus par m^2. En particulier, la biomasse absolue permet l'établissement de quotas à partir d'un seul inventaire à l'aide d'une table de décision. Alors que les inventaires d'abondance relative sont basés sur des protocoles d'échantillonnage et des sites fixes, les inventaires d'abondance absolue peuvent être améliorés dans le temps, compte tenu de la technologie. De plus, ces inventaires peuvent être concentrés dans les régions d'intérêt principal pour la gestion et les nombres absolus de la population échantillonnée en fonction de la longueur avec des intervalles de confiance constituent des données d'entrée riches en information pour la modélisation. Nous proposons et testons un plan d'échantillonnage à transect pour estimer et cartographier la densité et la biomasse absolues d'ormeaux ou d'autres invertébrés sédentaires. Les plongeurs dénombrent et mesurent tous les ormeaux situés en dedans d'une bande de 1 m de part et d'autre d'un câble plombé de 100 m déployé par bateau. Le placement semi-systématique des transects fournit un échantillonnage spatialement représentatif dans des régions d'échantillonnage à frontières définies, ainsi que des données géostatistiques pour la construction de cartes avec courbes de densité et de taille moyenne des ormeaux. Nous avons testé l'efficacité de ce plan pour l'estimation du changement de la taille de la population dû à la récolte et pour l'identification de régions dans lesquelles la densité permet la pêche, à l'aide d'une expérience de pêche intensive, en utilisant des inventaires faits avant et après une récolte commerciale. Les estimations du changement de la population et de la répartition spatiale obtenues par le plan d'inventaire au câble plombé s'accordent avec les récoltes de l'expérience de pêche intensive.

[Traduit par la Rédaction]

Introduction

Abalone stocks have collapsed in the northeast Pacific (Farlinger and Campbell 1992), California (Parker et al. 1992), and Mexico (Guzmán del Próo 1992) and have globally exhibited a higher risk of stock collapse than other marine organisms. Abalone catch rates are often insensitive to varying levels of total population size (Prince and Hilborn

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1998; Gorfine and Dixon 2001), underestimating population declines. This apparent hyperstability occurs because abalone aggregate (Shepherd and Partington 1995; Dowling et al. 2004*a*, 2004*b*) and divers can visually target remaining, higher-density patches. Moreover, these higher-density aggregations provide a larger share of fertilized egg production because male and female abalone must be close, 1–2 m apart (Babcock and Keesing 1999), for fertilization in the water column to be successful. Thus, abalone is a resource for which sustainability risks are high, but where commercial catch rates are less informative for stock management (Breen 1992). Fishery-independent diver surveys therefore provide a principal means of monitoring abalone resource status globally.

Current abalone diver survey designs provide relative measures of stock abundance from diver transects or timed swims. This is the case in the three countries where substantial abalone fisheries remain (Table 1): Australia (Shepherd 1985; Gorfine et al. 1998; Mundy et al. 2005); New Zealand (Andrew et al. 2000); and South Africa (Tarr et al. 2000). The first generation of Australasian abalone survey designs used timed swims (Shepherd 1985; McShane 1994). These do not control for area searched and often show high variability in abalone counts among divers. Timed swims were replaced in Victoria, Australia, by radial transects, which yielded significantly more precise abundance measures (Hart et al. 1997; Gorfine et al. 1998).

For both timed swim and radial transect designs, relative measures of abundance are obtained from permanently fixed sampling locations distributed along the coastline. Yearly sampling at fixed locations addresses and controls for the highly variable, spatially complex distribution of abalone that arises from abalone aggregating within heterogeneous reef structures. For example, for the fixed-site abalone survey in Victoria, several hundred global positioning system (GPS) sample locations were selected on abalone fishing grounds, with one to five fixed-point locations selected for each. Here, local, bounded survey regions are not designated; rather, the overall sample of fixed locations is taken to be a relative abalone abundance index in each management zone for use in a yearly time series. This abalone abundance measure is relative, rather than absolute, because it is not representative in space and relies on the use of an identical diver survey protocol each year to obtain a yearly comparable measure.

At least five important drawbacks arise from abalone survey designs that provide estimates of relative abundance based on fixed sampling protocols and locations. (*i*) Estimates of average abalone density across the coastal zone are almost certainly biased towards overestimating mean abalone density, because sampling locations were selectively positioned in productive fishing grounds. (*ii*) Because specific survey boundaries are not drawn and the spatial distribution of sample locations is not systematic or random, the measures of abalone density from fixed sample locations cannot be assumed to represent the true abalone density on any specific temperate reef or fishing ground. (*iii*) All aspects of the survey sampling protocol, including the sample locations and sampling methodology, must remain constant through time. Changes to either the sampling locations or survey methodology would disrupt the relative abundance measure, thereby rendering it incomparable with previous years. Alternatively, changes to the design of a relative abundance survey require calibration of the new survey time series with that of the series being replaced. This is achievable only through the additional cost of undertaking parallel surveys over multiple years and is complicated by the additional variance inevitably introduced in calibrating, which requires a statistical model to relate the two relative abundance time series. Short overlap periods and generally high abalone survey sample variances mean that the error introduced by calibration can be substantial. (*iv*) Current fixed-site designs do not permit mapping of abalone density to assess how abalone are distributed on temperate reef habitat or how these abalone spatial distributions change over time. (*v*) Several years of repeated sampling must be undertaken before relative measures of abundance become informative, i.e., several years of the time series are required to establish a baseline for comparison with future years.

In contrast to the challenges posed from surveys predicated on providing estimates of relative abundance, fishery-independent surveys that provide estimates of absolute abundance convey numerous advantages for resource management. For example, these survey designs can provide estimates of total harvestable biomass by conducting a single survey from which fishery managers can set spatially explicit harvest quotas. This is perhaps best achieved in a formal risk-assessment framework that combines survey measures of harvestable biomass in a decision table (Punt and Hilborn 1997) with a set of decision rules. Using this approach, quotas can be established even in the absence of stock assessment models or reliable catch and effort data.

Additional advantages of estimating absolute abundance are obtained for modeling, improving surveys over time, and finer-scale spatial management. In fisheries where a model is used for stock assessment and quota setting, adding absolute survey population numbers as a data input would anchor the model estimates to a direct fishery-independent measure of total population size. Inclusion of such data would enhance the accuracy and precision of length-based model stock assessment estimates. Also, when improvements in survey technology become available, such as submersible video and the ability to stratify survey regions through habitat mapping, the survey design can be modified without disrupting the survey time series. This advantage arises because absolute abalone density is defined independently of any specific sampling protocol, with all valid measures of density being comparable. Although these advantages accrue to any sedentary benthic invertebrate (e.g., Leeworthy and Skewes 2007), they are especially relevant to supporting finer-scale spatial management of abalone populations for which there is increasing call (Prince et al. 1998; Worthington and Andrew 1998; Saunders et al. 2008).

Estimating absolute abundance and, subsequently, total harvestable biomass relies on the fulfillment of two key criteria. First, an absolute population density quantity (e.g., number of abalone or legal biomass per square metre) is only uniquely defined, and thus measurable, inside bounded survey regions. Thus, absolute survey estimates require a closed boundary, or set of survey strata, with the spatial coverage of each being specified. Second, the transect locations must be distributed such that the measure of density

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Table 1. Summary of fishery-independent diver survey designs for principal abalone fisheries worldwide.

Country or Australian state	Survey design or method	Sample locations	Survey measure of abundance: relative or absolute	Reference
South Africa	Strip transects	Fixed	Relative	Tarr et al. 2000
Victoria	Radial transects	Fixed	Relative	Gorfine et al. 1998
New South Wales	Irregularly shaped selected search areas	Fixed	Relative	Andrew et al. 1996
Tasmania	Transects inside a circle	Fixed	Relative	Mundy et al. 2005
New Zealand	Modified timed swims	Random	Relative	Andrew et al. 2000
South Australia	Timed swims	Fixed	Relative	Shepherd 1985
Mexico	Stratified quadrats	Random	Absolute	Rodríguez-Valencia et al. 2004
South Australia (western zone blacklip)	Stratified survey areas and modified leaded lines	Semi-systematic	Absolute	Chick et al. 2006
South Australia	Leaded lines	Semi-systematic	Absolute	McGarvey 2006
South Australia (southern zone blacklip)	Modified leaded lines	Semi-systematic	Absolute	Mayfield et al. 2004

and length frequency is spatially representative. Systematic or semi-systematic (Byth and Ripley 1980) distribution of sample locations inside bounded survey regions or inside each stratum achieves this requirement.

Among the first approaches to estimating absolute abalone density were point-distance methods (Officer et al. 2001). However, both field trials and simulation testing found this method to be biased for clustering populations (Byth 1982; McGarvey et al. 2005). Building on previous transect-based approaches (e.g., Sainsbury 1982; Clavier and Richard 1986; Rodríguez-Valencia et al. 2004), in this paper, we propose and test an alternative transect survey design (hereafter referred to as the leaded-line survey design) to measure absolute population numbers and biomass inside bounded survey regions.

To achieve this, we (*i*) provide a description of the leaded-line survey design, including the statistics and bootstrap algorithms used to estimate absolute abalone density, total population number, and biomass, with associated confidence intervals, (*ii*) test the performance by predicting the change in greenlip abalone (*Haliotis laevigata*, hereafter referred to as greenlip) population number of the new survey design through a fish-down experiment during which greenlip were harvested in a controlled manner by commercial divers, and (*iii*) provide decision tables from a survey of greenlip and blacklip abalone (*Haliotis rubra*, hereafter referred to as blacklip) that were used to inform quota setting, thereby providing an example of the method's use in quota setting. The fish-down experiment also provided the opportunity to compare spatially explicit survey biomass distributions with commercial harvesting patterns. In Discussion, we consider the implications of estimating absolute abundance for abalone resource management, discuss advantages and disadvantages of leaded lines as one method of absolute abundance survey, and suggest possible improvements.

Material and methods

Leaded-line survey design

The principal objective of the diver survey design proposed is to measure absolute abalone population density and sample length frequency from which harvestable biomass can be estimated. The survey design has several components: (*i*) a survey region boundary is drawn; (*ii*) sample locations are distributed semi-systematically within the survey region or within each survey stratum; (*iii*) a leaded rope line is deployed onto the bottom from the research vessel between each pair of preselected GPS positions at each sample location; (*iv*) divers descend in pairs to count and measure all abalone inside the two 1 m transects lying to either side of the leaded line; (*v*) abalone counts are used to estimate population density and length measurements combined with weight–length are used to estimate harvestable biomass inside the survey region; (*vi*) estimates of confidence interval and 10% confidence quantiles for survey estimates of density and biomass are generated using a two-level bootstrap; (*vii*) the biomass quantiles inside a decision table are used in quota setting and producing contour maps of (*viii*) mean density and (*ix*) mean body length (abalone shell length (SL)) across the survey region.

Specifications of the leaded-line sampling protocol are listed in Appendix A. Methods for calculating the leaded-line survey estimates of mean density and total harvestable biomass, with two-level bootstrap confidence intervals (CI), are given in Appendix B.

Study site

Waterloo Bay (Fig. 1), off Elliston, South Australia, was one of the first and historically among the most heavily exploited abalone fishing grounds since the 1960s. It has been the site of extensive abalone field study, including abalone habitat preferences (Shepherd and Womersley 1981), movement (Shepherd 1986*a*, 1986*b*), aggregations, and spawning relationships (Shepherd and Partington 1995; Dowling et al. 2004*a*, 2004*b*). The abalone populations in the Bay have collapsed twice under harvesting since the 1980s (Shepherd and Baker 1998; Morgan and Shepherd 2006), and the Bay was therefore closed to fishing during 1982–1986 and from 1995 onward.

Fish-down experiment

The performance of the leaded-line survey design was tested in a fish-down experiment to assess the ability of the survey design to measure change in abalone population size

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under harvesting. Two leaded-line surveys, yielding survey estimates of absolute population number of harvestable-sized greenlip, were undertaken before and after a known commercial harvest. Both surveys and the commercial harvest were undertaken in a bounded survey region of 1,343 km^2 covering the outer two-thirds of Waterloo Bay (Fig. 1) during September–December 2003. The same 32 leaded-line sample locations (Fig. 1) were sampled pre- and post-fish-down surveys, following the sampling protocol described in Appendix A. The number of abalone harvested, the times to the nearest minute, and the GPS locations of surfacing of each bag of abalone harvested by commercial divers were recorded by boat operators on all vessels participating in the fish-down harvest. Fishers removed greenlip abalone in the specified "harvestable size" range (≥130 mm shell length, SL).

Fish-down experimental statistics: testing survey estimate of change in population number under harvesting

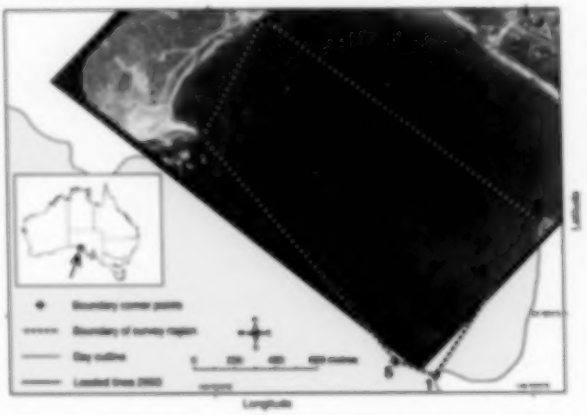
The statistical difference in population number from pre- to post-fish-down surveys was modeled by a difference bootstrap. This difference bootstrap was used to test the null hypothesis that the survey-estimated difference in harvestable-sized population number, from before to after commercial harvest, was not different from the known number of abalone removed by harvesters in the Waterloo Bay fish-down.

A bootstrap was chosen to statistically evaluate the difference in population number of the two surveys, in preference to a *t* test, which would have assumed that samples are normally distributed and independent. Neither assumption holds: (*i*) abalone survey density measures are generally skewed, with a large number of zero or low integer counts and a few relatively high counts; and (*ii*) the sampling hierarchy has two levels, with primary sample units being leaded-line locations and the secondary level of sampling being the two transect counts at each leaded line. A bootstrap approach was therefore used that makes no distributional assumptions and models the two-level sampling protocol. This bootstrap algorithm provides an unbiased statistical test of agreement between the survey estimate of abalone population change together with its 95% confidence interval (CI), which can be compared with the known number of abalone harvested. The difference bootstrap and associated fish-down experimental test statistics are summarized in Appendix C.

Mapping density and mean shell length

In addition to an estimate of mean absolute biomass averaged across the survey region, the measures of abalone density at sample locations (leaded-line centre points) distributed across each survey region provide spatial data for mapping of density or mean size. Because the sample locations are semi-systematic, they provide an approximately uniform grid of density samples, which is optimal for kriging and other geographic information system (GIS) contour mapping routines within the survey region. The density measure from the two transects combined at each leaded line (abalone count divided by 200 m^2 search area) was located on maps at the 50 m midpoint along each 100 m leaded line. Radial basis functions (ArcView Geostatistical Analyst, version 8.3; ESRI, Redlands, California) were used to generate the contour maps of survey absolute density and mean shell length. For commercial fish-down contour maps of catch per unit effort (CPUE) and mean length, kriging was used (ArcView Geostatistical Analyst, version 8.3). Cross validation and other statistical diagnostics informed the choice of contour mapping interpolation method.

Fig. 1. Map of the Waterloo Bay (South Australia) survey region with a rectified aerial photograph. The locations of the thirty-two 100 m leaded-line (pre- and post-fish-down in 2003) survey transects are shown. In the third 2005 survey, only leaded-line locations (numbered 1 to 20) were sampled.



Biomass survey to provide decision tables for quota setting

In 2005, commercial fishers requested re-access to Waterloo Bay, which had been closed to fishing since 1995. In response, the fishery management committee requested survey biomass estimates for greenlip and blacklip inside the 2003 fish-down survey region. By count and length measurements of greenlip in both transects at 20 leaded-line locations (Fig. 1), with simultaneous counts of legal-sized blacklip, estimates of harvestable-sized biomass were obtained for both species in a 2005 Waterloo Bay survey.

To frame the biomass estimates in a risk-assessment framework appropriate for quota setting, decision tables (Punt and Hilborn 1997) were produced from the leaded-line survey data for the two abalone species. Survey decision tables (Tables 2*a* and 2*b*) provide a quota value for each combination of chosen harvest fraction and estimate of available biomass to be taken. The latter are given in the nine columns of the decision table, each quoting a survey biomass estimate (top rows of Tables 2*a* and 2*b*) specified by 10%, 20%, …, 90% confidence probabilities that the true stock biomass equals or exceeds the quoted level. These leaded-line survey lower-bound estimates of harvestable biomass for each choice of confidence probability are estimated as the corresponding 10%, 20%, …, 90% quantiles from the two-level bootstrap (Appendix B). Two-level bootstrap replicates (10 000) were run for each species. Each row of the decision table corresponds to an assumed harvest fraction, the management-chosen proportion of each survey-estimated harvestable biomass to be allocated as quota.

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Table 2. Decision tables for quota setting. Inferred catch quotas (253 kg, 303 kg, etc.) under assumed levels of 90%, 80%, ..., 10% confidence probability that legal-sized biomass in the Waterloo Bay survey region is greater than or equal to the level shown in each column (5056 kg, 6051 kg, etc.) and assumed harvest fractions of 0.05 to 0.2 for (*a*) greenlip and (*b*) blacklip.

(*a*) Greenlip (kg).

	Survey biomass confidence probability (of lower-bound legal biomass estimate, kg)								
Harvest fraction	90% (5056)	80% (6051)	70% (6816)	60% (7503)	50% (8173)	40% (8822)	30% (9535)	20% (10 397)	10% (11 613)
0.05	253	303	341	375	409	441	477	520	581
0.075	379	454	511	563	613	662	715	780	871
0.1	506	605	682	750	817	882	953	1040	1161
0.125	632	756	852	938	1022	1103	1192	1300	1452
0.15	758	908	1022	1125	1226	1323	1430	1559	1742
0.175	885	1059	1193	1313	1430	1544	1669	1819	2032
0.2	1011	1210	1363	1501	1635	1764	1907	2079	2323

(*b*) Blacklip (kg).

	Survey biomass confidence probability (of lower-bound legal biomass estimate, kg)								
Harvest fraction	90% (11 676)	80% (13 696)	70% (15 237)	60% (16 667)	50% (18 041)	40% (19 500)	30% (21 173)	20% (23 144)	10% (25 852)
0.05	584	685	762	833	902	975	1059	1157	1293
0.075	876	1027	1143	1250	1353	1463	1588	1736	1939
0.1	1168	1370	1524	1667	1804	1950	2117	2314	2585
0.125	1460	1712	1905	2083	2255	2438	2647	2893	3232
0.15	1751	2054	2285	2500	2706	2925	3176	3472	3878
0.175	2043	2397	2666	2917	3157	3413	3705	4050	4524
0.2	2335	2739	3047	3333	3608	3900	4235	4629	5170

Note: The lower-bound survey estimates of biomass, in parentheses below each confidence probability, are taken as the 10%–90% legal biomass quantiles from 10 000 two-level bootstrap replicates.

Results

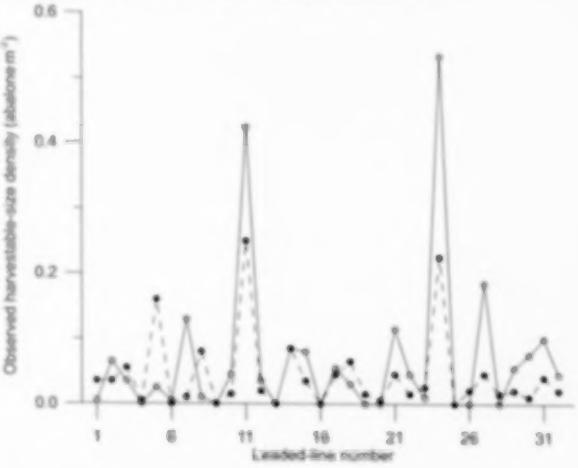
Fish-down experiment

The number density of harvestable-sized greenlip abalone in the Waterloo Bay survey region, from the November 2003 leaded-line survey run before the fish-down, was estimated to be 0.069 abalone·m^{-2}. When multiplied by the survey region area, this implies an estimate of 92 000 abalone (≥130 mm SL). These population estimates were from a total of 439 abalone counted and measured by divers in the 32 leaded lines (Fig. 2), each comprising two transects of 100 m^2. The two-level bootstrap standard error was ±31%, with zero counts at 21 of 64 transects.

After the fish-down harvest, the survey estimate of greenlip density declined to 0.044 harvestable-sized abalone·m^{-2}, a decline of 36%. The survey estimate of population size following the fish-down was therefore reduced to 59 000 harvestable-sized greenlip abalone. Standard errors of mean densities following the fish-down also declined from ±31% to ±24%. With reductions in both survey-estimated mean number density and its standard error as percentage of the mean, both greenlip abalone density and its standard error were substantially reduced under harvesting (Fig. 3). Divers counted 279 abalone above 130 mm SL, with zero counts observed in 16 of 64 transects.

The fish-down experimental result, using the difference bootstrap test, found statistical agreement of leaded-line survey difference from before to after fish-down with the known number removed. The number of abalone removed by harvesters (25 378) fell within a 50% CI, and well within a 95% CI, for the survey-predicted reduction in population of harvestable-sized abalone (33 500 ± 19 000) (Fig. 4).

Fig. 2. Number densities of harvestable-sized (≥130 mm shell length, SL) greenlip abalone (*Haliotis laevigata*) by leaded line in surveys run before (solid line with open circles) and after (broken line with solid circles) the 2003 commercial fish-down in Waterloo Bay. Each density point shown is an average of those from the two 100 m^2 transect counts at each leaded-line location.



Maps of density

Three maps of greenlip density in Waterloo Bay were generated in the fish-down experiment (Figs. 5*a*–5*c*) from

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Fig. 3. Confidence ranges for leaded-line survey estimates of absolute greenlip abalone (*Haliotis laevigata*) density. Box plots show the spread of bootstrap replicates for harvestable-sized (≥130 mm shell length, SL) number density from the two 2003 surveys run before and after the fish-down harvest. Quantiles of the 10 000 two-level bootstrap replicates are indicated by circles (5% and 95% confidence bounds), whiskers (10% and 90%), and boxes (25% and 75%).

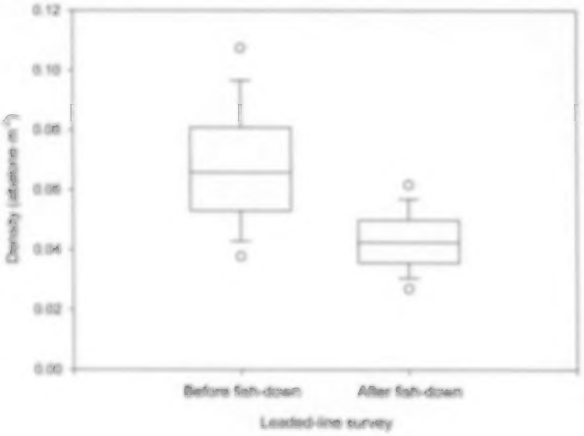
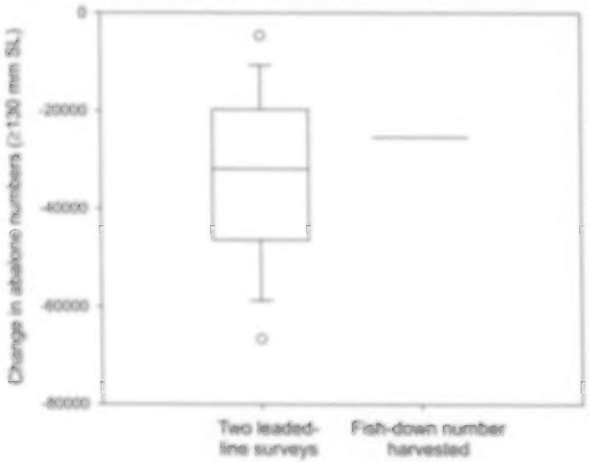


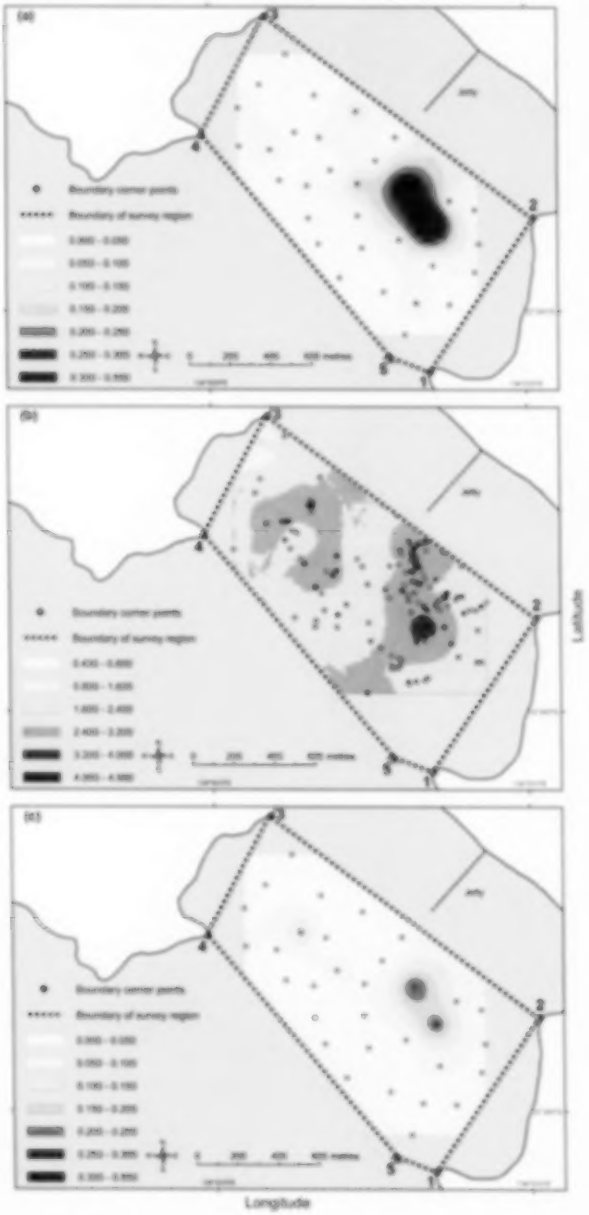
Fig. 4. Waterloo Bay fish-down experimental outcome. Box plot shows the distribution of 10 000 survey-estimated differences in legal population numbers from before to after the fish-down harvest, generated by the difference bootstrap. The box plot middle line, box, whiskers, and circles indicate quantiles of 50% (i.e., median), 25%–75%, 10%–90%, and 5%–95%, respectively.



pre- and post-fish-down surveys and from commercial fish-down CPUE. As a location-specific measure of density from the fish-down harvest, CPUE was quantified as the number of abalone by bag surfaced per minute.

One specific area of high greenlip density, south of the end of the jetty, was identified in both survey maps (Figs. 5*a* and 5*c*). This high-density area identified by survey overlapped closely with the area of high fish-down catch rate (contour shading of Fig. 5*b*). This same area was

Fig. 5. Contour maps of greenlip abalone (*Haliotis laevigata*) number density (abalone·m^{-2}) from the two leaded-line surveys: (*a*) before fish-down and (*c*) after fish-down. Only abalone of harvestable size (≥130 mm shell length, SL) were included in the survey density maps. The survey data were interpolated using radial basis functions. Points represent centre-point locations of leaded lines. (*b*) Contour map of catch rate from the Waterloo Bay fish-down commercial harvest where points (n = 140) represent location and catch rate of individual bags of harvested abalone (abalone numbers by bag divided by the harvest time in minutes). Contours for the fish-down catch rate data were interpolated by kriging.



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also where commercial fishing was primarily targeted (Fig. 5*b*, circles). By individual leaded line (Fig. 2), clear reductions in density were measured at the two high-density survey leaded-line locations, 11 and 24, lying in this hotspot. In comparing the survey contour map of greenlip density from before the commercial fish-down (Fig. 5*a*) with that generated by the survey after (Fig. 5*c*) the commercial fish-down, the comparison of surveys showed evidence of population decline in the specific area (Fig. 5*b*) where commercial fishing was principally targeted.

Thus two spatial trends in greenlip abalone distribution and abundance inferred from the two leaded-line surveys were consistent with the spatial pattern of commercial fishing and CPUE in the fish-down maps (Figs. 5*a*–5*c*): (*i*) high survey density in one specific location and (*ii*) reduced survey density after fishing in that location, confirmed by the observation that this is where fishing was primarily targeted. Thus it appears that a semi-systematic coverage of 32 leaded-line density measurements successfully located areas of high and low greenlip abalone abundance. Moreover, the population change under harvesting was described spatially, over a scale comparable with the distance between sample locations.

Maps of mean shell length

A consistent spatial trend was also observed in all three contour maps of mean greenlip shell length (Figs. 6*a*–6*c*). The two surveys and the fish-down identified a region of smallest mean size (lighter color) near the middle of the Bay (Fig. 6). This is consistent with the hypothesis and observations of Shepherd and Partington (1995) and Morgan and Shepherd (2006) that spat settlement is concentrated above this deepest part of the Bay in which water movement drogue studies (Shepherd and Partington 1995) suggest longer larval residence times as a consequence of slower and more circulating currents. Radiating outward from the central deeper-water zone were bands of increasingly larger greenlip abalone (Figs. 6*a*–6*c*). This is consistent with migration of abalone away from the central settlement zone as adults of larger shell length.

Thus two ecological hypotheses were supported by patterns in maps of size distribution of greenlip abalone in Waterloo Bay: (*i*) spat settle with higher probability in the central deeper water, and (*ii*) adults migrate, on average, away from the deep-water settlement zone to areas of higher bottom relief and faster water movement.

Biomass estimates for greenlip and blacklip abalone

The 2005 survey maps of biomass (Fig. 7*a*) show that the main area of densest greenlip, south of the jetty, had not changed since 2003 (comparing with Fig. 5). Surprisingly, blacklip abalone densities were also highest in this same location (Fig. 7*b*). Mean estimates of harvestable-sized biomass density in the Waterloo Bay survey region were 6.2 ± 1.9 and 13.8 ± 4.2 g·m^{-2} for greenlip and blacklip, respectively, increasing to about 14 and 50 g·m^{-2} respectively, in the high-density location.

Multiplying mean biomass density by the survey region area (1 343 235 m^2) yielded harvestable biomass estimates in 2005 of 8.3 tonnes (t) ± 31% standard error (SE) for greenlip and 18.4 t ± 30% SE for blacklip. The survey-estimated

Fig. 6. Contour maps of greenlip abalone (*Haliotis laevigata*) mean shell length (SL) from (*a*) the pre-fish-down leaded-line survey, (*b*) the commercial fish-down harvest, and (*c*) the post-fish-down leaded-line survey. Survey mean lengths (*a* and *c*) include only abalone of harvestable size (≥130 mm SL) for comparison with the mean length of abalone harvested in the commercial fish-down. The spatial data in (*a*) and (*c*) were interpolated using radial basis functions. Leaded-line locations where no abalone were found are indicated by green stars. For commercial mean length (*b*), each point (n = 140) represents the mean length of a surfaced bag of abalone, with contours interpolated by kriging.

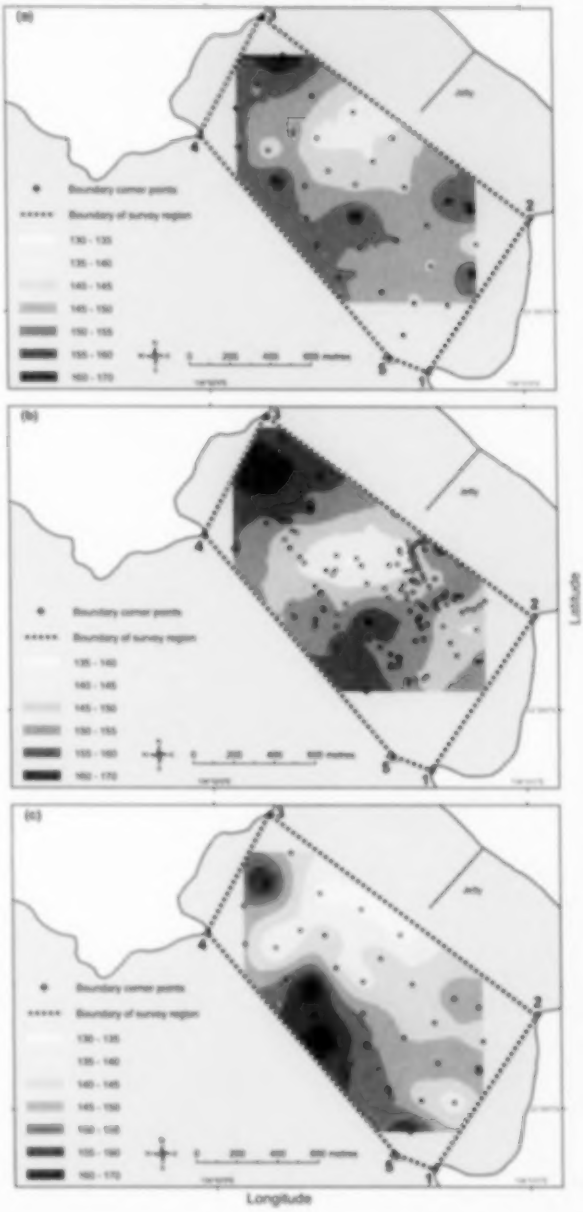

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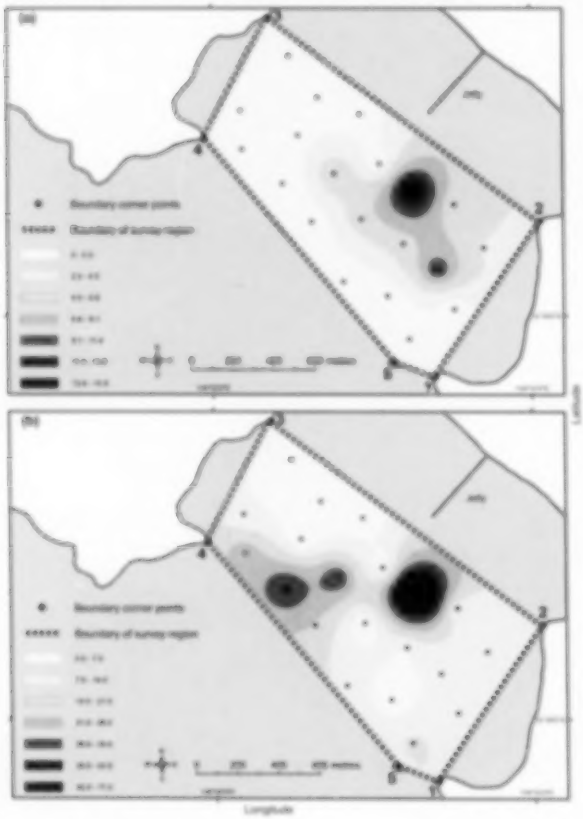
Fig. 7. Distribution of legal-sized (≥145 mm shell length, SL) biomass density ($g \cdot m^{-2}$) from the 2005 Waterloo Bay survey: (*a*) greenlip (*Haliotis laevigata*), and (*b*) blacklip (*H. rubra*) abalone. Circles indicate the midpoint of each leaded line ($n = 20$).



legal biomasses implied yearly quotas in decision tables (Table 2) that were much lower than anticipated. Industry and managers decided to leave Waterloo Bay closed.

Discussion

In this study, we presented the advantages of an absolute measure of density for abalone and other sedentary benthic invertebrates, proposed a diver survey design to measure absolute biomass and spatial distribution, undertook a fish-down experiment to test the performance of the proposed design, and gave an example of how the survey outputs could be used to set quota for management decision making.

The leaded-line survey design permitted representative sampling for absolute population density and length frequency. These served as inputs to estimate total harvestable biomass. Using the two-level bootstrap, the survey produced a range of likely biomass estimates specified by the probabilities of minimum biomass confidence level. From this range of biomass estimates, a quota decision table was generated.

The survey design and subsequent decision table were considered sufficiently robust by stakeholders to reach relatively rapid agreement in quota setting (e.g., Mayfield et al. 2008). In South Australia, the decision rule adopted thus far has been a 10% harvest rate of the 80% confidence probability leaded-line survey biomass estimate. The latter represents a conservative choice, requiring an 80% probability that the true biomass is equal to the assumed biomass or higher.

In practical application to abalone stock assessment and management, absolute abundance surveys offer numerous advantages. They (*i*) estimate harvestable-sized biomass for quota setting and (*ii*) are ideal for finer-scale spatial management. (*iii*) They can be run in designated abalone reefs of management interest, and (*iv*) the sampling design can be improved over time with stratification and new technology. (*v*) A 3- or 4-year baseline is not required before they become informative for stock management. (*vi*) Most model assumptions and prior assumed rates such as natural mortality and growth are not needed to estimate survey biomass, but (*vii*) when used as model input, direct survey measures of total population numbers by length would increase model accuracy, notably of absolute population size. Survey contour maps of abalone (*viii*) population density and (*ix*) mean length can be drawn by interpolation, and (*x*) measures of absolute density and short-term clustering of abalone or other sedentary invertebrates offer previously unavailable performance indicators for risk assessment and stock management.

Management implications

Surveys of absolute abalone abundance offer managers access to a wider range of useful information and opportunities, including the ability to set quota from the estimates of total harvestable biomass and to develop new time series indicators of fishery performance, permitting management at relevant, often finer, spatial scales by mapping abalone distribution and body size.

Quota setting

Fishery quotas are often set as a percentage of an estimated harvestable biomass, whether obtained from a survey or model. To date, for abalone, estimates of biomass for quota setting have been primarily obtained from length-based models in New Zealand (Breen et al. 2003) and Australia (Worthington et al. 2001; Gorfine et al. 2005), fitted to survey measures of relative abundance, survey length-frequency samples, and commercial catch and effort data. The absolute level of population size can be difficult to precisely estimate by length-based models because it is inferred through an indirect form of model inference, namely by interpreting length samples through a growth submodel, in combination with catch totals.

These survey outputs can be used in the absence of a model, or in combination with one. When a direct survey measure of absolute biomass is available, it can replace modeling, the only means previously available for estimating biomass, avoiding errors that length-based models might introduce. This also saves the cost of producing a model, or it can provide a measure of biomass when modeling capability is not at hand. For abalone, model error can result from a number of circumstances that make abalone stock assessment challenging, namely high spatial variation in growth, an often hyperstable relationship of stock biomass

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to commercial CPUE, the relatively indirect inference of mortality rate from length-frequency samples combined with an assumed growth submodel fitted separately to tag recovery data, variation in the length selectivity of the commercial catch, under-reported catch totals mainly due to poaching, and an assumed constant natural mortality rate. None of these assumptions or assumed constants is needed when biomass can be measured directly.

With biomass estimated from a single survey, in particular using the decision table approach, a natural precautionary strategy can be implemented by setting quota, in the first instance, using a conservative decision rule. In subsequent years of stock management and quota setting, with periodic surveys and observation of how the stock responds under survey-measured percentages harvested, the quota can be modified under this form of adaptive management (Hilborn and Walters 1992), with increasing knowledge from this iterated experience made possible by repeated survey measurements of absolute biomass.

In addition to estimating biomass, stock assessment models can be used to address other questions that managers would raise. When a model is used, absolute survey data can refine quota setting, with model estimates of biomass made more reliable by fitting to survey measures of total abalone population numbers by model length bin, with confidence intervals, anchoring model estimates to a direct survey measure of absolute population size.

Performance indicators

Over time, the accumulated knowledge of how abalone populations respond under different survey-measured levels of harvest fraction and absolute population density can be used to better establish decision rules for how much can be safely taken and when a population has a higher risk of decline. Survey measures of absolute density permit systematic comparison of stock sustainability among different abalone reefs or fishing grounds or with published estimates of abalone density (Rogers-Bennett et al. 2002, 2004). We can hypothesize that low absolute abalone density will signal higher sustainability risk, but this must be tested in future applications of absolute abalone surveys. By relating stock decline risk to the mean or spatially dependent absolute density of abalone on a reef, the density of abalone provides a performance indicator for stock assessment and management that is not available with relative abundance survey designs.

When abalone counts along each leaded-line transect are recorded in 1 or 2 m quadrats (McGarvey 2006), a measure of spatial clustering is obtained. A measure of clustering over 1 to 100 m spatial scales can inform the risk of local densities being too thin to permit successful fertilization in the water column during spawning events (Babcock and Keesing 1999). This capability can serve to monitor the impact of fishing on fertilization success (Levitan and Sewell 1998), providing a performance indicator that quantifies abalone spatial aggregation on 1 to 100 m distance scales.

Spatial management

The semi-systematic allocation of transect-pair samples inside bounded survey regions provides a spatial grid of density and mean body size data for contour maps. Mapping abalone distributions (as absolute number or biomass density per square metre) permits spatial management on the scale of distances between leaded lines up to the extent of each survey region, or between survey regions. Finer-scale spatial management of abalone populations, specifically the setting of reef- or subregion-specific size limits and quotas, is being implemented in South Australia and Victoria because population growth rates and density vary substantially over medium (within-reef) spatial scales (Saunders et al. 2008). Semi-systematic samples inside bounded survey regions permit this finer-scale spatial management. Surveys can be directed to management subregions of chosen size and location. Fixed sample sites distributed permanently along the entire coastline cannot be flexibly deployed for this purpose and generally do not provide data useful for mapping.

Over longer time scales, maps of abalone distribution serve to address one of the principal hypothesized causes of hyperstability in abalone stock assessment, namely spatial contraction of local populations while density within patches remains more nearly constant, leading, hypothetically in some stocks, to collapse (Shepherd and Rodda 2001; Shepherd et al. 2001). Like schooling of fish, spatial contraction permits abalone catch rates to stay high as the total population declines (Breen 1992; Prince and Hilborn 1998). Mapping abalone density provides a way to monitor the broad-scale spatial distribution of abalone subpopulations, including spatial contraction.

Advantages of leaded lines

Among possible survey designs that estimate absolute population density, several advantages of the leaded-line method are notable. (*i*) It affords divers no choice about where to search in counts of abalone. (*ii*) The variation in 2 m quadrat counts (when recorded) along each leaded-line transect permits the short-scale spatial clustering of abalone to be quantified. (*iii*) It provides a self-weighted and thus representative length-frequency sample. (*iv*) The time that research divers would spend underwater deploying a transect cable and recovering it is saved, permitting more bottom time for population measurement. (*v*) A long, thin sampling geometry reduces spatial autocorrelation, providing a more representative sample of abundance at each sample location. Points *i*, *iii*, and *v* are elaborated below.

By deploying the leaded line from the boat, all research diver choice about where to search is removed. In previous surveys (McGarvey 2006), four 25 m perpendicular transects were added to the 100 m leaded-line transects at each sample location, survey divers manually deploying transect cables perpendicular to the leaded lines. Density estimates from the perpendicular transect along cables laid by divers were significantly higher ($P = 0.006$) by 11% than densities measured in the regular transects lying along the boat-deployed leaded lines where no diver choice was possible. The use of a boat-deployed transect cable avoids any overestimation bias that divers controlling where transect lines are laid may inadvertently introduce.

In addition, count variability among survey divers can be substantial. Prepositioning a stiff, weighted transect line onto the bottom reduces the effect of diver variability by more strictly controlling the search area. Requiring divers to

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follow a prepositioned leaded line and choosing a visually evident point on the abalone shell (the "spire", Appendix A) for determining inclusion or not of each animal inside the transect removes potential measurement error among divers, providing a more reliable diver-independent measure of abalone density at each leaded-line sample location.

A representative length-frequency sample within each bounded survey region is obtained with this design for two reasons. First, the sample size of abalone measured for length from each leaded-line sample location is self-weighted. More abalone at a location implies correspondingly more abalone, on average, counted and measured for length. Length-frequency sample size is thus, on average, weighted by local population density. This is achieved when sampling is representative in space. Second, because the semi-systematic grid of samples covers the survey region uniformly, sampling is spatially distributed with similar area surrounding, and thus similar area of the sample frame covered by each length-frequency sample.

By choosing a long, thin sample geometry, which directs diver sampling along a 100 m leaded line rather than among shorter transects distributed inside a circle as done in Victoria and Tasmania, the mean distance between all samples (say, between all 1 m^2 quadrats) is maximized, whereas for transects arrayed inside a circle, the mean distance between sample quadrats is effectively minimized. A greater average distance among sample quadrats should yield lower survey sample variances by averaging across more patches of high and low density in each diver transect, yielding abalone counts spanning wider stretches of reef. Thus, higher survey precision, countering high spatial autocorrelation due to clustering of abalone, favors a transect geometry of long, thin lines.

Disadvantages of leaded lines

Undercounting bias

Some abalone will be missed by research divers searching in some transects, creating an underestimation bias in the survey estimate of absolute density and thus also of biomass. Undercounting is considered to be small (compared with sample variance) for legal-sized greenlip (≥145 mm SL), which are found openly on more flat and less vegetated reef habitats, but blacklip are often cryptic in high-relief bottom and undercounting for blacklip could be significant, especially for sublegal sizes.

Because of survey undercounting and because the 10% to 90% decision table quantiles are, by definition, cumulative probabilities that the true biomass lies equal to or above the corresponding survey quantile biomass so estimated, the survey measures of absolute harvestable-sized biomass in decision tables used for quota setting are understood as lower-bound estimates. Thus, the true biomass equals or, in practice, exceeds each survey biomass estimate tabulated with designated (bootstrap-derived) probability.

High variation in proportion legal

In management practice, notably for quota setting, estimates of biomass or population density are needed specifically for the legal-sized range of abalone. A larger-than-expected variation in the proportion of legal-sized abalone was observed in previous fish-down experimental surveys (McGarvey 2006). This measured population ratio, call it the "proportion legal", is a binomial random variable. The proportion legal among sample locations varied much more than a random binomial null distribution would have implied, consistent with previously observed high variation in length samples (Pennington and Vølstad 1994; Pennington et al. 2002). When abalone shell lengths are measured separately from the transect counts, or when in some transects divers record quadrat counts rather than shell length measurements, a single parameter of proportion legal must be estimated from the subsample of abalone that were measured for length. This estimated parameter of proportion legal is then multiplied by the overall density measure to estimate legal-sized density. Thus, high uncertainty in the proportion legal parameter increases the sample variance of the estimates of legal-sized density and thus total harvestable biomass.

This added source of binomial error is minimized by adopting a survey protocol wherein all abalone counted in every transect are also measured for length. Given the lengths of all surveyed abalone, the legal biomass sum or population count from each transect is restricted to include only the legal-sized animals. In this way, no parameter of overall proportion legal need be estimated to estimate harvestable biomass, and error from spatial variation in the proportion legal induced when this proportion is approximated by a single measured value for the survey region overall is not incurred.

Future improvements

Stratification

Stratification is a promising strategy for improving survey precision in future years. This is achieved by habitat mapping and refined contour mapping to identify high-, medium-, and near-zero-density abalone areas based on previous years of density survey. Survey precision can be optimized by a Neyman allocation of leaded-line samples (Cochran 1977), placing more leaded lines in strata of higher abalone density and higher sample variance. GPS – depth loggers attached to commercial divers (Mundy et al. 2005) can provide highly resolved spatial information about where fishing occurs, informing stratification and survey boundary placement (Mayfield et al. 2006).

Power analysis

The reduction observed in survey sample variance subsequent to harvesting in the fish-down experiment at Waterloo Bay is consistent with earlier studies (Breen 1980; Hart et al. 1997). Vézina (1988) reported an allometrically increasing sample variance with increasing mean density for a range of marine benthos with an exponent of about 1.2. Breen (1980) estimated this exponent at 1.5 for British Columbian abalone. Fishing hypothetically reduces variance because fishers target the highest density patches. This observed trend of sample variance, increasing slightly more than linearly with mean density, using, for example, Breen's exponent for abalone under harvesting of 1.5, could be used in future power analysis and survey design.

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Applications

Now applied in South Australia, the leaded-line design is used in the central and western zones for greenlip abalone surveys. Two variants of the leaded-line survey design have also been successfully implemented for blacklip in the South Australian southern (Mayfield et al. 2004) and western zones (Chick et al. 2006). At Cowell, this approach was combined with commercial exploratory harvesting over a systematic checkerboard grid to estimate greenlip biomass and set quota in a region spanning 1100 km^2 (Mayfield et al. 2008). The survey method has recently been adapted in Western Australia for estimating greenlip abalone biomass in proposed marine protected areas (Hesp et al. 2008). The advantages of the leaded-line survey design suggest its applicability to a broader range of sedentary benthic invertebrates.

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Appendix A. Leaded-line survey diver sampling protocol

Specifications of the leaded-line survey sampling protocol are as follows.

1. Spatial information about the area to be surveyed is assembled. Maps of depth, substrate type, and vegetation are consulted before drawing survey region boundaries. GIS layers of the coastline and depth contours and of catch and effort statistical reporting blocks serve as the underlying map on which the "survey region" boundary is drawn. The survey region can also be stratified.
2. The boundary of the survey region is drawn in a GIS layer. GIS software also provides a calculation of the surface area (m^2) covered by each bounded survey region or each stratum.
3. Leaded-line transects are located semi-systematically, i.e., spatially distributed uniformly inside the survey region or inside each stratum.
4. Usually, leaded lines are drawn parallel to the prevailing currents to assist diver movement.
5. A map of the study area with semi-systematic leaded-line positions (Fig. 1) is drawn and provided to research divers before departure. Start and finish positions of leaded lines to be swum are entered into the onboard GPS chart plotter.
6. Leaded lines, 100 m long, of stiff brightly colored nylon rope woven with lead are deployed onto the bottom from the boat between all pairs of GPS positions specified. The line that the divers used was rigid, providing a consistent 100 m length. Distances along the length of the leaded rope are marked every 2 m.
7. Two divers descend and swim on either side of the leaded line. Survey diver effort and safety are optimized (*a*) by swimming with the prevailing current and (*b*) with divers operating in pairs swimming side-by-side.
8. Each diver swims on one side of the leaded line searching a 1 m × 100 m transect. All abalone with the spire (peak point) of their shell lying within 1 m of the leaded line are counted and measured for shell length. Divers reported that 1 m was a comfortable transect width of bottom to search. Any wider would require sidewise swimming movement, which is highly inefficient.
9. Divers can optionally provide more highly spatially resolved density measures, to a 1 m scale, by recording abalone counts in successive 1 or 2 m quadrats along the 1 m wide leaded-line transects. In practice, divers could only comfortably record 2 m quadrat counts by foregoing the measurement of abalone shell lengths.
10. All vegetation is pushed aside, but no rocks are overturned.

Appendix B. Calculating mean density with confidence intervals for the leaded-line two-level sampling design

Here we describe the bootstrap algorithm used to quantify confidence interval and produce confidence quantiles of abalone population number or biomass inside survey regions using measurements from the leaded-line diver survey design. Number density is measured in each diver transect as the count of abalone (overall or within any chosen length subinterval) divided by the search area. To calculate biomass density in each transect, the average landed meat weights of all legal-sized abalone were summed, using the length–weight relationship applied to each measured individual. By restricting the biomass density sum to legal-sized abalone and using a weight measure consistent with landed quota, survey estimates of biomass available for harvest are calculated in the same abalone weight units used to set quota.

Mean density in the survey region for the two-level sampling design was calculated by (*i*) averaging the density measurements from the two transects lying on both sides of the line to obtain the mean density at each leaded-line sample location and (*ii*) averaging these two-transect means across all leaded-line locations in each survey region or stratum. This estimate of density can be in numbers or biomass within any specified abalone size range.

Confidence intervals for this survey estimate of mean density were estimated using a bootstrap, resampling with replacement from the leaded-line density measurements (Efron and Tibshirani 1993). There are two important advantages of a bootstrap: (*i*) it makes no requirement that the data be normally distributed, in fact, no predefined family of distributions is required, unlike with likelihood or Bayesian methods, and (*ii*) it can be applied effectively to any chosen estimator of mean density, including those from survey designs with complex sampling hierarchies.

Estimating the confidence interval for mean density was done using a two-level bootstrap. This quantifies random variation at both levels of the sampling hierarchy by resampling (*i*) from among the primary sample units of leaded-line sample locations and, then, (*ii*) from among the secondary sample units of individual density measurements, namely the two transects at each resampled leaded line. Bootstrap resampling at these two levels of the survey hierarchy quantify "between-primary-unit" and "within-primary-unit" sample variance (Cochran 1977).

The nature of these two levels of sample variation are distinct. At the between-primary-unit level, each leaded line is at a separate location, and thus, each provides a separate measurement of density that reflects the spatial variation of abalone distribution across the study region. The within-primary-unit counts from the two transects at each leaded line are understood as repeated measurements at each location. Bootstrap resampling at two levels models both sources of sample variation in estimating confidence intervals for the survey estimate of mean abalone density.

The two-level survey sample data sets from which boot-

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strap samples are drawn are the diver-measured (abalone number or biomass) densities within each transect. Each resampled two-level bootstrap replicate produces a single estimate of mean density in the survey region, a "possible" outcome for resampled survey mean density. This bootstrap method can be extended to account for stratification or any other modification of the sampling protocol.

Bootstrap replicates (10 000) of mean density were drawn. The standard error of mean density was calculated as the standard deviation of bootstrap replicates. Quantiles from the set of bootstrap replicate mean densities or biomass (i.e. 5%, 25%, 50%, 75%, and 95%) were formed, giving 1%, 5%, etc., confidence intervals. Lower-bound confidence intervals for biomass over the range from 10% to 90% were used in quota decision tables (Table 2).

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Appendix C. Fish-down experimental test statistics

A "difference" bootstrap was designed and used to quantify confidence intervals for the estimated change in absolute legal population number from the two surveys run before and after the fish-down harvest. The difference bootstrap 95% CI underlies the statistical test of whether the survey-estimated change in population number of harvestable-sized abalone agreed with known number harvested. If the known number removed fell within the survey difference 95% CI, the survey estimate was said to be in agreement.

The difference bootstrap algorithm incorporated two two-level bootstrap algorithms (Appendix B), those from pre- and post-fish-down surveys individually, to quantify the uncertainty in their difference. Using survey data of mean legal population number in each transect of the two surveys, a difference bootstrap of 10 000 replicates was run to quantify the survey-difference confidence range.

The difference bootstrap algorithm for leaded lines is summarized as follows. For each replicate, (*i*) a two-level bootstrap resample of leaded lines (primary level of sampling) and sides of each leaded line (secondary level) was drawn for the pre-fish-down data set, as described in Appendix B. (*ii*) This same set of randomly resampled leaded-line numbers and sides of each leaded line was used for post-fish-down survey resamples in each bootstrap replicate to simulate the experimental protocol of the same leaded-line locations being swum by divers for both pre- and post-fish-down surveys. (*iii*) A survey estimate of absolute legal population number was calculated from the bootstrap resample, using the two-level mean of Appendix B, for both pre- and post-fish-down survey data sets. (*iv*) The two estimates of absolute legal greenlip population size were then subtracted to obtain the difference, one predicted difference for each bootstrap resample. (*v*) The standard deviation of the (10 000) bootstrap estimates quantifies the standard error on the estimated change in survey-estimated absolute density from before to after removal by commercial divers. (*vi*) The number of abalone actually removed by commercial divers was taken to be the reported number, assumed known without error.

Confidence intervals of 50%, 80%, and 90% were constructed using the quantiles of difference bootstrap replicates over 25% to 75%, 10% to 90%, and 5% to 95%, respectively (Fig. 4). More generally, $(100 - 2\alpha)\%$ confidence intervals are defined by the lower and upper α quantiles of the bootstrap estimates of abalone mean density or biomass.

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Salmonid or nonsalmonid lakes: predicting the fate of northern boreal fish communities with hierarchical filters relating to a keystone piscivore

Johan Spens and John P. Ball

Abstract: We determine if lacustrine salmonids show large-scale patterns of coexistence with the keystone predator northern pike (*Esox lucius*) and test an approach to predict fish communities using coexistence rules set in the context of three hierarchical filters that a species must pass to be present. The mutually exclusive species distribution patterns that we detected among 1029 lakes were repeatedly verified from results of whole-lake interventions with rotenone and introductions. Essentially, pike did not coexist with self-sustaining salmonid populations in lakes. High connectivity to pike (derived from maps) largely predicts the absence of lacustrine salmonids. Our analysis strongly suggests that pike prevented self-sustaining populations of brown trout (*Salmo trutta*), Arctic char (*Salvelinus alpinus*), and brook trout (*Salvelinus fontinalis*) in lakes. High connectivity to pike resulted in nonsalmonid lake fish communities, most often including both European perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*). Our analysis suggests that if pike were not present in many boreal lakes where they now dwell, salmonid fish assemblages would prevail, a sharp contrast from the present pike-driven homogenized state with mainly nonsalmonid fish communities.

Résumé : Nous déterminons si les salmonidés lacustres possèdent des patrons de coexistence à grande échelle avec le brochet du nord (*Esox lucius*), leur prédateur le plus important, et nous testons une méthode pour prédire les communautés de poissons à l'aide de règles de coexistence qui comprennent trois filtres hiérarchiques qu'une espèce doit traverser pour être présente. Les patrons de répartition des espèces mutuellement exclusives que nous avons détectés dans les 1029 lacs se vérifient à répétition lors d'interventions à la roténone ou d'introductions à l'échelle des lacs entiers. En somme, les brochets ne se retrouvent pas avec des populations autosuffisantes de salmonidés dans les lacs. Une forte connectivité avec le brochet (déduite à partir de cartes géographiques) permet la plupart du temps de prédire l'absence de salmonidés lacustres. Notre analyse indique clairement que le brochet empêche l'établissement de populations autosuffisantes de truites brunes (*Salmo trutta*), d'ombles chevaliers (*Salvelinus alpinus*) et d'ombles de fontaine (*Salvelinus fontinalis*) dans les lacs. Une connectivité au brochet produit des communautés de poissons lacustres sans salmonidés, mais contenant souvent à la fois la perche (*Perca fluviatilis*) et le gardon (*Rutilus rutilus*). Notre analyse laisse croire que si le brochet était absent de plusieurs lacs boréaux où il habite présentement, il y aurait prédominance de peuplements de poissons salmonidés — en contraste marqué avec l'état d'homogénéité actuel des communautés de poissons non salmonidés, causé par le brochet.

[Traduit par la Rédaction]

Introduction

Understanding the main factors that determine the distribution of species is critical for the effective conservation and management of many ecosystems. For freshwaters, a promising tool for predicting species' distributions is the use of series of hierarchical filters (Poff 1997; Quist et al. 2005) that a species must pass to be present in a given location (Tonn et al. 1990). A promising avenue to construct this filtering framework may be to focus on taxa that are strong interactors (i.e., "keystone species"; Poff 1997) like some predators or competitors. We propose that barriers to the dispersal of keystone species, i.e., (*i*) keystone-focused connectivity, used in sequence with (*ii*) abiotic habitat characteristics followed by (*iii*) coexistence rules with keystone species, can advantageously be used as three hierarchical filters for predicting fish communities in lakes.

A previous single-species study predicted the distribution of the keystone species northern pike (*Esox lucius*) (hereafter pike) with very high accuracy (86.6% correct classification among 1365 lakes), mainly based on a map-derived connectivity variable (Spens et al. 2007). Specifically, in this earlier paper, a geographic information system (GIS) derived variable (S_{V5max}) that quantified dispersal barriers to pike provided a measure of steepness in relation to 5 m (vertical) contour intervals rather than the traditional measure of rise over a fixed, and typically long, length of stream. For example, the conventional measure would quantify a rise of so many metres per 100 m, or 200 m, of river or whole stream and is less suited to differentiate a gradual slope, which would not impede dispersal, from a waterfall, which would. In contrast, the S_{V5max} variable will indicate a dispersal barrier whenever there was a rise of 5 m (i.e., in ≤76 m or ≥6.6%) for pike; this figure is empirically derived in Spens et al. 2007). Thus, this previous study shows that con-

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nectivity may be a very strong filter, and we use it here as the first of our three hierarchical filters. Passage through this first filter is required for a species to be exposed to the next filter.

Secondly, pike show remarkably wide tolerances for abiotic factors and environmental conditions, a tendency that contributes to their wide circumpolar distribution in subtropical to arctic waters (Craig 1996). Pike occupy a broad latitudinal belt (40°N–70°N), are distributed throughout most of Europe (from sea level up to the Alps, with a successful introduction at 1400 m), Siberia to Kamchatka in Asia (Inskip 1982; Raat 1988), and in 45% of North American freshwaters (Casselman and Lewis 1996). Thus, for pike, abiotic factors may represent a relatively nonconstraining filter because of their tolerance for a wide range of environmental conditions. Nevertheless, passage through this second of three hierarchical filters is required to potentially influence other species in a given lake.

Pike are keystone piscivores that are important in "top-down" structuring of fish communities (Casselman and Lewis 1996). They have been associated with lowering prey fish abundance in slow-flowing streams (Rincon et al. 1990; Degerman and Sers 1993; Näslund et al. 1998). More dramatic effects are observed in lakes: pike are associated with extinctions of fish species (e.g., small-bodied fishes, Robinson and Tonn 1989; threespine stickleback (*Gasterosteus aculeatus*), Patankar et al. 2006; Arctic char (*Salvelinus alpinus*), Byström et al. 2007; brown trout (*Salmo trutta*), Spens 2007). Surprisingly, to our knowledge, no peer-reviewed empirical field study has focused on or quantified pike-driven extinctions of salmonids at a large scale as we do here. There are, however, several indications from the grey literature and from studies citing government sources in northwestern America that pike are a major threat to salmonids (McMahon and Bennett 1996; Dalton 2002) (although not specified, these alleged threats to native west coast salmonids most likely refer to *Oncorhynchus* spp.). Salmonids are among the most pursued freshwater species by anglers (e.g., in 2001, 37.5% of all freshwater anglers in the United States sought salmonids; Leonard 2005). Consequently, they are of vital importance as a leisure resource and considered to be catalysts for economic growth. Thus, accumulating information suggests that pike, from both an economic and ecological viewpoint, is a leading candidate for an important keystone species that may drive crucial coexistence rules, the third and last of our three hierarchical filters.

Based on the three concepts above, we evaluate if three hierarchical filters (all focused on a keystone species (Post 1997), here pike) may predict which lakes will support salmonid or nonsalmonid (in our area, mostly percid- and cyprinid-dominated) fish communities. Our first step is to explore connectivity (focused on pike) in a landscape-scale study among more than 1000 lakes containing pike and (or) salmonids. Our second step is to compare to what extent a "classic approach", which mainly considers water quality and other abiotic in-lake factors as the driving force in governing the fish community (e.g., salmonids are found in oligotrophic lakes, nonsalmonid fish communities in more eutrophic ones), actually predicts the fish community. Thirdly, we explore landscape-scale coexistence patterns of fish species among lakes and then assess the causes behind any observed patterns by using empirical long-term results of hundreds of whole-lake salmonid and pike introductions and removals.

Material and methods

Study area

This study (1985–2007) includes pike and salmonid lakes (n = 1029) and connected streams situated within watersheds covering 7650 km^2 centred near 63°36′N, 18°10′E in the northern boreal region of Sweden. The lake district is a result of deglaciation 9600 years ago. Our investigation included 23 complete (e.g., Moälven, Nätraån, Husån, Idbyån, Näskeån, and Strömsån) and eight partial river drainage basins (e.g., Ångermanälven, Gideälven, Lögdeälven, and Dockstaån), each terminating independently in the Baltic Sea. The landscapes range from coastal to inland, including hilly as well as flatter productive forestland, to low slope wetlands and agricultural areas. Lakes range from clear to dystrophic and mostly oligotrophic to mesotrophic, although there are several eutrophic lakes in areas with agriculture. A majority of lakes belong to 63 Fishery Management Organisations (FMOs hereafter) that also provided information about the fisheries.

Connectivity

Connectivity was determined by GIS following the empirical method of Spens et al. (2007). "Low" connectivity lakes (i.e., those with barriers to pike movement) were defined as those with an $S_{VSmin} \geq 6.6\%$ or having SSBs (subsurface streamflow through bouldery areas, i.e., where a stream is restricted to only subsurface flow through boulders, a barrier through which pike do not move) or artificial barriers to fish movement like impassable dams or seepage lakes with WC-elev (defined here as elevation above the nearest connected water with $S_{VSmin} < 6.6\%$) ≥ 3.5 m. "High" connectivity lakes had $S_{VSmin} < 6.6\%$ or were seepage lakes with WC-elev < 3.5 m. Three initially undetected outlet streams of lakes on topographic maps were corrected from field observations. In 28 lakes where pike had been established by known introductions (thus circumventing natural barriers), only the preintervention fish community was used to determine the accuracy of connectivity classifications. Because of geographic overlap, 65.3% of the lakes included in the single-species connectivity model validation presented in Spens et al. (2007) were also included in our current multispecies study, which includes 137 additional lakes.

Abiotic factors

To determine to what extent lake characteristics might explain salmonid–pike occurrence patterns, we extracted additional potential explanatory variables (Table 1) in accordance with widely held ecological views of northern boreal lakes. Lake area and shoreline length were determined digitally from polygon-vector shapefiles, corrected in some cases by aerial photographs and field observations. Wetlands, i.e., stillwater basins with maximum water depths <2 m (limit for initial emergent macrophyte growth), were not included in our study of lakes. The range of lake

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Table 1. Abiotic characterization (the second hierarchical filter) of salmonid (S) and nonsalmonid (NS) lakes and discriminatory ability of logistic regression.

	n		Mean		SE		Minimum		Maximum		Logistic regression		
Variable	S	NS	S	NS	S	NS	S	NS	S	NS	McFadden's R^2	*P*	TSS
pH (units), ±0.5%	163	376	5.9	6.0	0.03	0.02	5.0	4.6	7.0	7.1	0.03	<0.001	0.04
Alkalinity (mequiv. L^{-1}), ±2%	162	376	0.07	0.11	0.01	0.01	0.0	0.0	0.66	1.34	0.04	<0.001	0.05
Colour (mg Pt L^{-1}), ±6%	172	394	102	86	4	3	0	3	383	393	0.02	<0.01	0.02
Total phosphorus (µg L^{-1}), ±10%	105	184	10	13	0.4	0.7	3	3	29	71	0.04	<0.01	0.04
Lake area (ha), ±3%	250	779	15	49	4	6	0.1	0.2	840	2780	0.05	<0.001	0.05
Shoreline length (km)	250	779	1.52	3.38	0.14	0.25	0.1	0.2	26	143	0.06	<0.001	0.06
Maximum depth (m), ±4%	170	279	11	14	0.5	0.5	2	2	48	53	0.02	<0.001	0.03
Mean depth (m), ±7%	133	219	4.5	5.0	0.2	0.2	1.4	0.7	14.1	17.5	0.00	ns	0.00
Altitude (m) < 1%	250	779	270	214	5	3	20	0.1	455	431	0.06	<0.001	0.06

Note: McFadden's R^2 (McFadden's rho squared (between 0 and 1)) is a transformation of the likelihood ratio statistic intended to mimic R^2. TSS (true skill statistic (between 0 and 1)) is an alternative measure of model performance independent of prevalence (Allouche et al. 2006). TSS = sensitivity + specificity − 1. R^2 or TSS values close to 0.00 indicate that the model performs no better than chance. Note that measurement error with 95% confidence interval is given after the parentheses, except for altitude where the mean measurement error is given after the parentheses. ns, not significant.

sizes included is illustrated in Fig. 1. Maximum depth (n = 449) and mean depth (n = 354) of lakes were determined by measurements with an echosounder from a boat or sounding line from ice. Altitude was determined from a digital elevation model and topographic maps of Sweden at a scale of 1:50 000, with elevation contours produced from aerial photogrammetry. Mean annual air temperature (1921–2005) was 0 °C at 500 m altitude to 3 °C at sea level (Swedish Meteorological and Hydrological Institute 2006).

Water chemistry data were measured in 572 lakes between 1985 and 2007. Water was sampled in the lake centre under ice with a Ruttner sampler at 2 m depth during stable winter conditions, on average 9 March. Mean values were calculated for those lakes sampled in multiple years, and for limed lakes, only preliming data were used. We measured pH at 20 °C in the laboratory according to Swedish standard SS 028122-2. Alkalinity was measured while aerating with N_2 and titrated past pH 5.4 according to SS EN ISO 9963-2c. Total phosphorus was estimated by digesting a water sample with potassium peroxysulphate and determined colorimetrically using a molybdate buffer according to SS 028127-2. Colour was measured with a spectrometer in a 5 cm cuvette at a wavelength of 420 nm according to SS EN ISO 7887 (400 nm before 1994). Swedish standard methods for water chemistry are available from the Swedish Standards Institute, 118 80 Stockholm, Sweden (e-mail: info@sis.se).

All scale variables were log-transformed except pH and altitude, which appeared, by inspection, to be normally distributed. Correlations among morphometric and water chemistry variables of lakes are common, and our data were no exception (e.g., variance inflation factors were between 5 and 21 for two-thirds of these variables). We used SYSTAT's (2002) missing value procedure, which uses Buck's (1960) algorithm to impute estimates for missing values in the multivariate analysis: only 14.2% of the abiotic data on lakes were so affected, and no critical data dealing with the fish community, stocking, connectivity, or whole-lake manipulations were affected. We examined relationships between salmonid occurrence, water chemistry, and lake morphometry variables one by one (to permit comparison with previous studies) with simple logistic regression and collectively with multivariate logistic regression.

Fish species

We used several methods and gathered information from a number of sources to comprehensively validate fish species presence–absence. Face-to-face in-depth interviews with representatives of local FMOs or other well-informed persons were conducted from 1985 to 2007 to collect information on current species distributions, introductions, and extinctions in all lakes. Data were sought from at least two corroborating primary sources to evaluate fish species presence–absence. To obtain more reliable data, interviews clearly established each informant's area of knowledge and allowed the collection of data only within their expertise. We used presence–absence data as recommended by Jackson and Harvey (1997), which are less prone to impacts of ordinary cyclic environmental change (e.g., daily or annual variation) than abundance data and facilitate comparison of data collected using different methods and

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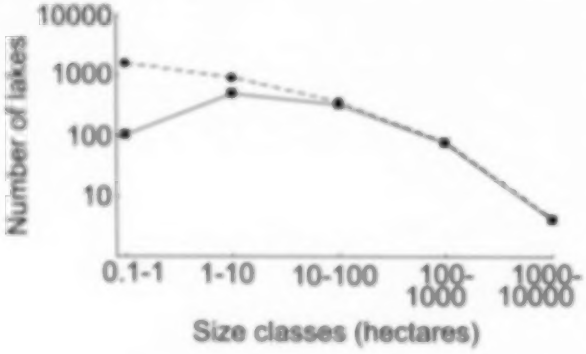
Fig. 1. Range of lake sizes (log scale). The solid line (squares) indicates the range of lake sizes included in our study and the broken line (circles) indicates the complete set of lakes situated within our study area. Catches and reports of northern pike and salmonids are lacking from many of the smallest lakes, ponds, and wetlands, so this size class is reduced in our study. Note, however, that we have data for all of the larger water bodies in our area and that for the smaller water bodies, our sample sizes are still quite large, so our conclusions are unlikely to be an artefact of the sizes of lakes we analysed.



sources, and reduce the risk of overinterpretation in lake fish community studies.

Historical records of fish species distribution from 1552 to 2007 and stocking between 1868 and 2005 were obtained from three major forest companies, county administrations, municipality administrations, FMOs, the National Board of Fisheries, and other sources. We also collected lake names from maps of 1672–1968 (Spens 2007) where archaic terms used for brown trout were found to fully support our historical baseline data of brown trout distribution. Three hundred and eight lakes within the study area were surveyed from 1985 to 2006 (mode 2000) with multimesh-sized gill nets according to Appelberg (2000) or with a slightly modified sampling stratification. In addition, we surveyed most lakes (n = 919) with other methods, e.g., angling, single-mesh-sized gill nets, and trapping (1985–2007), to further verify the data. We verified extant salmonid populations and their reproduction in tributaries and outlet streams (apart from Arctic char, whose fry was only found in lakes) by electroshocking or angling. This intense effort to identify lakes where fish were reproducing allowed us to test for true coexistence (i.e., self-sustaining populations) of salmonids and pike by allowing us to exclude lakes with nonreproducing populations that were only artificially sustained by stocking (potentially a critical difference from many previous studies). In this study, we considered coexistence patterns among all lakes with pike or (and) self-sustaining salmonids.

Note that we considered all species within the family Salmonidae in our study area (brown trout, Atlantic salmon (*Salmo salar*), brook trout (*Salvelinus fontinalis*) (exotic), Arctic char, rainbow trout (*Oncorhynchus mykiss*) (exotic), and European grayling (*Thymallus thymallus*)) because they have similar ecology and are closely related (monophyletic; Nelson 2006). We did not include the Coregonidae (e.g., whitefish (*Coregonus* spp.)) in this group because their ecology differs considerably (e.g., defence against predators; e.g., Balon 1975) and one may even choose to recognize them as a separate family (Nelson 2006).

We defined a salmonid lake as one containing a self-sustaining salmonid population in enough numbers to be caught repeatedly by, e.g., angling, gillnetting, or trapping, and that were not merely "transit lakes" (i.e., with only seasonally occurring sea-run salmonids moving between sea and spawning streams). This definition was not particularly restrictive and excluded just 27 lakes (among which were eight transit lakes and 16 lakes that had exactly one single historical record of a salmonid observation within the last 50 years and in which no additional salmonids were detected during our test fishing or in reports from FMOs despite substantial fisheries). We acknowledge that our investigation, like all others, cannot determine absence with absolute certainty, only nondetectability. Overall, however, we suggest that there is only a small chance that we failed to detect salmonids among those lakes classified as salmonid-free waters from our combined test-fishing efforts, extensive interviews with local fishers, and contacts with FMOs (who, of course, market and sell licenses for the higher priced and more carefully managed salmonid fisheries and thus are very eager to report any evidence of salmonids). We are sure, however, that any such undetected salmonids provided no significant value to the fisheries (FMOs would have to be unaware that their lake held these highly coveted salmonids). Most importantly, we suggest that any salmonid population that we failed to detect must be of such low density that there is little chance that salmonids would have an important ecological role in that lake's fish community. In perch-free lakes (where salmonids were reported in interviews or caught in our other surveys), detectability of salmonids was 100% with our survey effort. In lakes where European perch (*Perca fluviatilis*) were present, our detectability was nearly as high (96% using minimum 0.3 and mean 1.2 multimesh-sized gill nets per hectare). Our quality control regarding pike confirmed that pooled test-fishing surveys (multimesh-sized gill nets with a catchability of 89.1% complemented by single-mesh-sized gill nets, trapping, and angling) were in close agreement with pooled interviews and historical documents, differing in less than 1.4% of all lakes.

Interventions: introductions, rotenone, and subsequent recolonizations

A key part of our data was not merely observational, but in fact the results of whole-lake manipulations (Table 2). Records of introductions of salmonids into lakes with pike and into lakes where pike were removed by rotenone provided an opportunity to evaluate the importance of this key piscivore to the establishment of self-sustaining salmonid populations in lakes. To test the importance of dispersal barriers to pike, we contrasted the resulting fish community in lakes with high versus low connectivity after pike were eradicated by rotenone. The long-term results of salmonid and pike introductions were revealed by interviews and historical documents and verified by test fishing with multimesh-sized gill nets or other fish-sampling methods, e.g., electrofishing and trapping.

We assessed interventions by counting the number of affected lakes that had altered presence–absence of salmonids,

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Table 2. Overview of sample sizes and the number of lakes in both the tests of landscape (large-scale patterns) and interventions (whole-lake manipulations).

Data sets	Lakes (n)
Landscape (large-scale patterns)	
First filter, connectivity determined with a prior empirical model	1029
Second filter, multivariate analysis of abiotic factors (univariate n = 289–1029 lakes)	531
Second filter, separate multivariate and univariate analysis of lakes where salmonids extinct	33
Third filter, tentative analysis of coexistence, assumed salmonid access to all 781 pike lakes	1029
Third filter, conservative analysis using only those lakes with verified salmonid access, i.e., salmonid lakes and only those pike lakes directly connected to grayling streams (n = 53), receiving streams from lakes with Arctic char (n = 40) or trout	554
Interventions (whole-lake manipulations)	
Salmonids introduced (range years: 1902–2000, n = 936, 1–58 yearly introductions per lake, mean = 5.9, SE = 0.7):	
to pike lakes	160
to high-connectivity (n = 59) and low-connectivity (n = 44) lakes after pike were removed with rotenone*	103
where potentially confounding effects from removal of other fish species with rotenone was controlled with (re)colonizing species from, e.g., pike-free untreated lakes upstream: perch (n = 3), burbot (n = 5), ninespine stickleback (*Pungitius pungitius*) (n = 6), and crucian carp (*Carassius carassius*) (n = 3) into low-connectivity lakes with introduced salmonids	17
Pike introduced to pike-free salmonid lakes	28

*The regular dosage was 0.5 mg (L lake volume)$^{-1}$.

while we used the true skill statistic (TSS) (Allouche et al. 2006) to assess predictive performance of each hierarchical filter. Logistic regression (SYSTAT 2002) and model selection with Akaike's information criterion (AIC) (Burnham and Anderson 2002) were used to model abiotic factors (the second hierarchical filter), while we used the binary predictions (presence–absence of fish community) from connectivity and pike to evaluate the first and the third filter, respectively. The number of lakes in our data sets used to evaluate filters and interventions is listed in Table 2.

Results

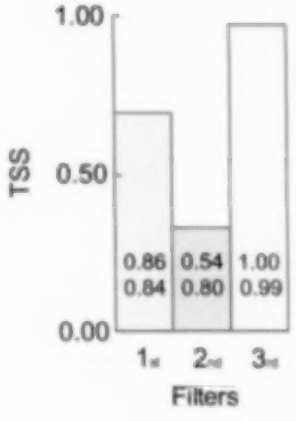
First hierarchical filter: connectivity for a keystone piscivore

Most strikingly, 660 (95.2%) of 693 lakes with high connectivity had pike. However, pike were also present in 121 low-connectivity lakes, resulting in a total prediction accuracy of 85.1% in predicting pike from just GIS data in all 1029 lakes (Fig. 2). Using field surveys, we discovered SSBs (undetectable by GIS), which would prevent pike from colonizing most of the remaining lakes that were erroneously predicted as having pike using S_{VSmax}. After these field surveys of barriers, only 3 of 663 lakes with high connectivity lacked pike, indicating that any additional filters at lower hierarchical levels (subsequent second and third filters) were almost entirely open to pike.

Second hierarchical filter: abiotic filter

Because the first filter proved so effective in our study area, there was little utility in constructing a second filter from only three pike-free lakes with sufficient connectivity. Thus, we only report detailed test results of possible bias from lake characteristics for the salmonid occurrence pattern and for salmonid extinctions. Altitude (as an index of climate) and in-lake habitat, i.e., water chemistry and lake morphometry, covered a wide range of values (Table 1). In-lake habitat did not explain much of the incidence of salmonid communities in lakes. In a univariate approach, logistic regression for each individual variable predicted the fish community quite poorly (Table 1; among all variables, maximum McFadden's $R^2 \leq 0.06$, $P < 0.001$; maximum TSS $\leq$ 0.06). Similarly, the multivariate approach using logistic regression and stepwise model selection (via AIC) again did not predict the fish community very well (Fig. 2).

Fig. 2. Model performances (true skill statistic, TSS) of individual hierarchical filters. First filter: connectivity from GIS, n = 1029; second filter: in-lake abiotic factors by multiple logistic regression of nine in-lake habitat variables, n = 531, AIC = 465.5, the top model performance out of the five best parsimonious multiple logistic regression models with the lowest AIC values is illustrated; third filter: salmonid – northern pike noncoexistence rule, n = 554. Sensitivity (% correctly predicted presences) is the upper number inside the bars and specificity (% correctly predicted absences) is the lower number inside the bars. TSS = sensitivity + specificity – 1. Left bar, filtering pike; middle and right bars, filtering salmonids.



Furthermore, water chemistry did not separate 33 lakes where we found that salmonids had gone extinct (mainly in conjunction with introductions of pike) from lakes where salmonids persisted: using logistic regression for each indi-

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vidual variable, the maximum value of McFadden's R^2 was <0.01 and TSS was 0.0, indicating very poor predictive ability. Turning our attention to the five lakes where pike had not been introduced, where no barriers had been constructed, but where all salmonids had gone extinct, we found that pH separated these lakes from those lakes where at least one salmonid species still persisted (median pH 5.0 versus 5.8, respectively, McFadden's $R^2 = 0.62$, $P < 0.05$). Four of these five lakes were later recolonized by salmonids after liming, initiated by our survey results.

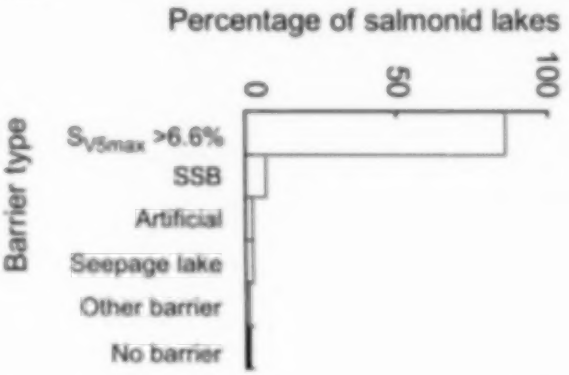
Third hierarchical filter: coexistence patterns

The third hierarchical filter was redundant for modelling patterns of pike occurrence. This was indicated by our preceding first hierarchical filter in that pike had access to merely three additional lakes where they were now absent. Pike were present in lakes dominated by the region's most common fish species, perch, roach (*Rutilus rutilus*), and burbot (*Lota lota*), but pike were occasionally allopatric. In nonsalmonid lakes, roach and perch did not co-occur unless pike were present. Perch or roach often also co-occured with salmonids. We modelled salmonid communities directly using coexistence pattern with pike (the third filter) because we tentatively assumed that the first and second hierarchical filters to pike lakes would also be passed by salmonids. We consider this is a reasonable assumption because they show superior dispersal ability (pike are limited by $S_{V5max} \geq 6.6\%$) and because abiotic conditions measured in our study did not differ much between salmonid and nonsalmonid lakes (Table 1 and multivariate analysis of nine variables (Fig. 2)).

Salmonid lakes were inversely predicted from pike lakes, as we found an almost perfect mutually exclusive occurrence pattern of pike without salmonids ($n = 779$) and with salmonids ($n = 2$) and salmonids without pike ($n = 248$). Among these 248 lakes without pike, the sum of sympatric and allopatric salmonids was 307. Considering this on a species-specific basis, this was brown trout (215), Arctic char (15), brook trout (75), rainbow trout (1), and grayling (1). Nearly all of these lakes had low connectivity downstream isolating them from potential source populations of pike. The types and proportions of barriers downstream of these salmonid lakes are illustrated in Fig. 3.

To further verify our rather striking results, we also produced a second, more conservative model estimate of the pike–salmonid coexistence pattern. To do this, we included salmonid lakes and only those pike lakes situated downstream of salmonid waters or that had directly connecting streams where we verified salmonid recruitment (thus assuring that absolutely every lake in this more conservative model was accessible to salmonids) (Table 2). This model exhibited essentially the same high accuracy (Fig. 2) as when all 1029 lakes were included. There were only two misclassified lakes with coexisting pike and salmonids (i.e., brown trout and brook trout), and these were among the very largest lakes (upper third percentile). In addition, we note that pike and self-sustaining salmonid populations (Atlantic salmon, grayling, and brown trout) were sympatric in the Baltic Sea (442 000 km^2) in which all drainages finally terminate. The near-perfect, mutually exclusive occurrence pattern of pike and salmonids is illustrated with a connectivity chart representing lakes in the Husö-basin in Fig. 4.

Fig. 3. Types of barriers downstream of 248 salmonid lakes without northern pike. Open bars, proportion of salmonid lakes with barriers; solid bar, misclassified lakes (with no barriers to pike populations).



Interventions: introductions, rotenone, and subsequent recolonizations

Whole-lake interventions demonstrated repeatedly that pike (not salmonids) drove the third filter and thus evidently determined community composition. Every salmonid introduction but one (at 383 m altitude) failed to establish a self-sustaining population in 160 lakes with pike, while pike survived these interventions. However, in lakes where pike were removed by rotenone (provided that there was a low pike-specific connectivity preventing post-rotenone recolonization of pike from populations located downstream), salmonids did establish in 59% of lakes ($n = 44$). Considering this on a species-specific basis in all 103 rotenone lakes, this is brook trout (61% success, $n = 23$), brown trout (54% success, $n = 41$), Arctic char (19% success, $n = 27$), grayling (8% success, $n = 12$), Atlantic salmon (0% success, $n = 3$), and rainbow trout (5% success, $n = 22$). Furthermore, salmonid establishment in these lakes with lower connectivity (where pike failed to recolonize) increased to 100% success ($n = 25$) if populations of respective salmonid species became established in connecting streams.

Examining possible confounding effects from removal of other fish species in lakes where pike were removed with rotenone (Table 2), we verified that these (re)colonizing fish species did not prevent successful establishment of salmonids when pike failed to recolonize. In lakes with higher connectivity (e.g., $S_{V5max} < 6.6\%$ and no impassable SSB or artificial barriers) from potential pike source populations, we found that pike had recolonized and salmonids never established ($n = 59$). Among these, for every recolonization that only involved allopatric pike ($n = 11$), the consequences for salmonids were exactly the same as when associated species such as perch, roach, or other species recolonized together with pike ($n = 48$). Finally, every case of pike introduction into salmonid lakes always eliminated the entire lacustrine salmonid community. Given the pike-driven relationship with salmonids, as revealed by filters and interventions, and the nonconstraining second filter among our study lakes, we

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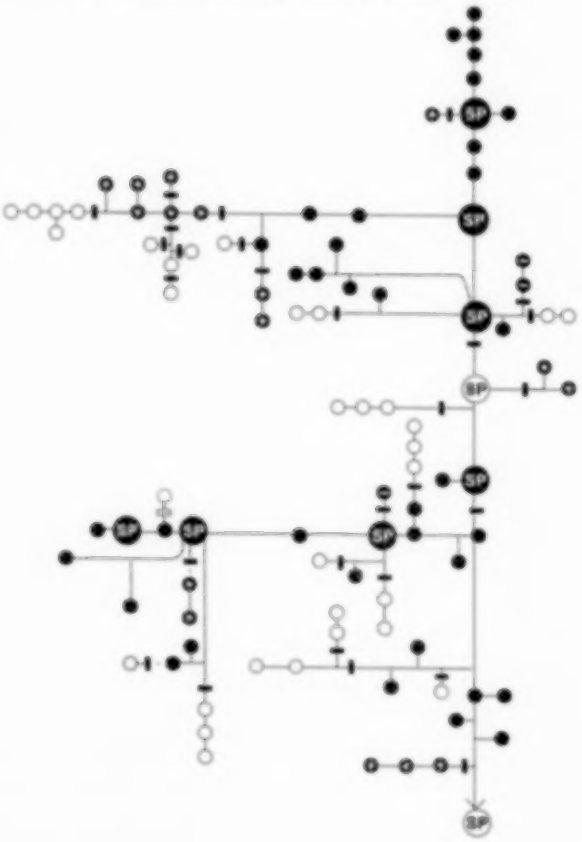
Fig. 4. Graphic chart of connectivity among the network of salmonid ($n = 31$) and northern pike ($n = 66$) lakes in the Husá-basin. Large circles (SP) are potential source populations of pike (predicted postglacial refuges; Spens et al. 2007) and starting points in the linear analysis of connectivity. Large open circles represent a lake (middle SP circle) and the sea (bottom SP circle) with both salmonids and pike. Follow SP lakes upstream to the first barrier, as well as downstream all the way to the sea, to predict pike presence lakes. Solid circles are lakes with pike. Residual lakes, i.e., small open circles, are salmonid lakes, all where pike are excluded. Shaded circles represent lakes with pike that were not correctly predicted with GIS (UC model sensu Spens et al. 2007). Plus signs are lakes with pike present that we predicted ($n = 10$) with the UC model to be introduced populations and lakes where pike were confirmed ($n = 6$) to be introduced, including former salmonid lakes. Minus signs are lakes where pike had been extirpated by rotenone and pike failed to recolonize, now stocked with salmonids. Solid bars represent migration barrier indicators ($S_{\mathrm{VSmm}} \geq 6.6\%$). One open bar represents a migration barrier (SSB) that was not predictable with GIS. The arrow points to the sea in the streamflow direction. Lakes lacking both pike and salmonids, located upstream of this illustrated network of lakes, are not included in the figure. Each right angle along interconnecting lines represents a subbranching into a smaller tributary from any drainage stem.



found it logical to simply predict the presence–absence of salmonids from pike connectivity. Note that high connectivity is associated with the presence of pike, and our analysis revealed that pike and salmonids essentially did not coexist. Thus, high connectivity indicated the absence of salmonids (model accuracy from GIS data was 0.85).

Discussion

Piscivore rules

Our results suggest that an improved understanding of the fundamental determinants of fish communities in boreal freshwater lakes may be attainable using a keystone-focused approach (here, with three hierarchical filters that a species must pass to be present). For the first hierarchical filter (connectivity), we used a recently developed method (S_{VSmm}: map-derived connectivity for pike) for obtaining connectivity to the key piscivore (also see Spens et al. 2007). In our current study, S_{VSmm} explained 86% of all exclusions of pike from salmonid lakes, and when we complement this with field observations of SSBs (subsurface streamflow through bouldery areas, i.e., where a stream is restricted to subsurface flow through boulders, a barrier through which pike do not move) and artificial barriers, the percentage explained rises to 95%. Thus, pike distribution was almost completely predictable from the knowledge of barriers to them (i.e., "pike have to be able to reach a given lake", the first hierarchical filter).

In waters with sufficient connectivity to allow pike access, the second hierarchical filter (abiotic factors) was usually passed because pike colonization is currently little limited by in-lake abiotic factors within our study region. Neither did this filter (i.e., the "classic approach") contribute much to predicting our fish communities. However, in general, we suggest that abiotic factors should always be included in the hierarchical approach that we advocate (i.e., "a fish population must be self-sustaining in the abiotic conditions associated with a given lake", the second hierarchical filter). For example, we could not rule out that low pH may have acted as a filter in a few lakes (2% of salmonid lakes) where all salmonids had gone extinct.

A third hierarchical filter is strongly indicated from landscape-scale species distributions among lakes in our study, as coexistence of salmonids and pike was very rare and salmonid lakes could be inversely predicted from pike lakes with extremely high accuracy. In addition, the driver of this highly effective third hierarchical filter is revealed from the results of repeated manipulations at the whole-lake level that very strongly suggest a deterministic piscivore effect (e.g., salmonids established in only 1 of 160 lakes where pike existed, but in lakes where pike were removed by rotenone, salmonids established in the majority of lakes where there were barriers to pike recolonization). In short, as a general rule, salmonid introductions fail to become self-sustaining in lakes if pike are present (pike introductions consistently eliminate lacustrine salmonid populations): "the pike–salmonid noncoexistence rule". Whole-lake removals of pike with rotenone repeatedly validated this apparently deterministic piscivore effect and that it can be reversed if pike-focused connectivity is low enough to stop recolonization of pike. In most such lakes, low connectivity then allows for establishment and long-term persistence of self-sustainable salmonid populations in lakes. Overall, then, our analysis reveals a piscivore-driven noncoexistence

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rule that (with some exceptions, see below) predicts "elimination of salmonids in lakes with pike". Ours is the first empirical study known to us that quantifies this critical effect of pike presence on salmonid communities.

That the mechanism of this noncoexistence rule is predatory exclusion is further supported by evidence from several independent radiotracking studies where predation by pike reduces the number of stocked brown trout (length 27–32 cm) by 50% or more within 4–7 days in still waters (Gönczi et al. 1986; Hyvärinen and Vehanen 2004). In contrast, mortality from pike of larger brown trout (≥36 cm) was only 5%, although in this case, most survivors emigrated out of the study area within 3 days (Hyvärinen and Vehanen 2004). Similarly, prey emigration out of a lake following the introduction of pike was shown to be of at least equal importance as actual consumption by pike (He and Kitchell 1990).

Many factors are involved in the structuring of fish communities, and we must emphasize that here we consider only the most fundamental aspect: species presence–absence per se; we anticipate that extended models involving abiotic filters may prove more useful at lower levels (e.g., when predicting species biomass when presence has been established). The species composition in freshwater ecosystems has often been explained by biotic factors (i.e., predations and competition) and abiotic factors (i.e., physical and chemical) as well as scale and spatial factors (see review by Jackson et al. 2001). Overall, they concluded that there is more convincing evidence for piscivory by fish as the main factor affecting the community composition than there is evidence for competition. They found that large-scale studies support the importance of abiotic controls (cf. connectivity in our study). These abiotic controls dictate the importance of piscivory, thereby indirectly influencing the composition of prey species present. Our current study thus provides strong evidence from a large-scale study to support Jackson et al.'s (2001) generalization from both our landscape patterns and long-term results from our manipulations (i.e., introductions, rotenone eliminations, and observations of the fish community that reestablishes). Protection from piscivores in "safe havens" formed by natural landscape fragmentation from impassable barriers in drainage networks has been recognized as necessary for the persistence of diversity in other fish communities worldwide (e.g., small-bodied fish species diversity (Robinson and Tonn 1989); galaxiid diversity (Townsend 2003); cichlid diversity (Mbabazi et al. 2004)). Thus, we suggest that low-connectivity river networks may fulfil a crucial role in maintaining biodiversity by allowing sensitive species safe havens by filtering off detrimental biotic interactions. Just as the importance of high connectivity for anadromous fishes is widely recognized, our results lead us to emphasize that ecologists and managers must also be aware of the importance of low, key piscivore focused connectivity for maintaining lake species diversity, especially salmonid diversity.

Why has the large-scale pike–salmonid pattern, so clearly evident in our analysis, not been described in the scientific literature before? Stocking of salmonids is widespread in temperate lakes (e.g., McGurrin et al. 1995; Tammi et al. 2003). We suggest that the mutually exclusive relationship between self-sustaining salmonid populations and pike may have been masked by this stocking activity (in other words, what may have been perceived as salmonid populations in other studies have not been self-sustaining populations but artificially sustained by stocking, e.g., in Tammi et al. 2003). To a lesser extent, salmonid transit lakes (i.e., those with a seasonal short period when sea-run salmonids co-occur with pike) may also have masked this pattern in previous research. Unlike these previous studies, our extensive data verification and subsequent analysis excluded transit and nonsustaining artificially stocked salmonid lakes, and our analysis strongly suggests that, at least in our large data set, most lacustrine salmonid populations are rarely self-sustaining in the presence of pike; we observed coexistence in 0.2% of lakes and in 0.3% of all whole-lake manipulations.

Our study was carried out among lakes located well within the temperature range of pike and barely included potentially marginal pike habitat at higher altitude (maximum 455 m) and latitude (maximum 64°N). One of the two lakes with coexisting pike and salmonids was situated in the colder upper margin of our study. As pike are primarily mesothermal (Casselman and Lewis 1996), low temperatures will constrain them more than coldwater salmonids. For this reason, we expect that pike and salmonid coexistence will be more common at the upper cold margins of pike distribution approaching 70°N latitude (the northern limit of its range) and within its range in alpine regions. This pattern was indicated by Flick (1977) who stated that pike and brook trout coexistence is observed in northern but not in southern lakes. However, cases of severe impact from introduced pike on salmonids suggest that our observations of pike-driven coexistence patterns may still apply to wide geographic regions (e.g., Ireland (Went 1957; Igoe et al. 2003); Spain (Rincon et al. 1990); Great Britain (Maitland and Campbell 1992); northwestern United States (McMahon and Bennett 1996); California (Moyle 2002); Alaska (Dalton 2002)).

It is also important to note that a lake-size-dependent, piscivore-driven coexistence rule has been suggested for certain small-bodied cyprinids, which do not coexist in small temperate lakes with piscivores such as pike. However, as the size of lakes exceeds 150–200 ha, there is a trend towards coexistence (see Jackson et al.'s (2001) reference to unpublished data in that paper). However, in our data, pike and salmonids coexisted in only two lakes, so we find little evidence for such a lake-size-related trend among these lakes. On the other hand, we know that there are lakes outside our study area (in colder lakes, towards the upper boundaries of the pike's range) where pike and considerable salmonid populations coexist. In addition, coexistence is also common in running waters, although here, pike are mainly present in slower flowing sections. It is also common knowledge that in warmer climates, there is coexistence in large and deep lakes (e.g., in the Great Lakes of North America and a number of lakes in Europe). At present, we lack information on what factors make coexistence possible in these waters. We therefore suggest additional studies to determine to what degree a finer second hierarchical filter (i.e., less favourable abiotic in-lake habitat for pike, e.g., relatively larger pelagials and (or) colder lakes) may relax our binary noncoexistence rule. Furthermore, the importance of

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weak acidic water for impairing detection of chemical alarm cues by salmonids (Leduc et al. 2006), potentially involving dietary odours of predatory pike and also coexistence, needs to be tested among lakes. We also suggest additional studies to reveal factors that promote high recruitment of large salmonids from pike-free areas (i.e., refuge areas where salmonids can grow to exceed the gape-size limits of pike). Such factors might modify the noncoexistence rule from binary to continuous. In future research on climate warming effects on salmonids, it will also be crucial to measure the first hierarchical filter, i.e., pike-focused connectivity. For example, by evaluating this within our study area, we can rule out pike expansion in all but possibly three salmonid lakes in the face of climate warming because of these barriers to the spread of pike.

High connectivity promotes a nonsalmonid fish community

Our analysis revealed that pike were nearly exclusively present in lakes with nonsalmonid fish communities, mainly dominated by the two most common species of the region, perch and roach. In nonsalmonid lakes, roach did not co-occur with perch unless pike were present. This may indicate that pike predation relaxes some severely negative perch–roach interaction (an idea in agreement with inference from whole-lake experiments; Persson et al. 2007). Our analysis suggests that high connectivity for pike promotes the development of a nonsalmonid-dominated community, while more limited connectivity may allow salmonid communities refuge. In contrast, a widely held ("classic") concept is that water quality determines structure of fish community assemblages: salmonids are associated with high water quality and thus dominate the clear oligotrophic lakes, and coregonids and perch succeed each other in mesotrophic conditions, while they are successively replaced by cyprinids towards eutrophy (Colby et al. 1972; Ryder and Kerr 1978; Persson et al. 1991). Eutrophic–mesotrophic lowland systems have milder elevation gradients and thus higher connectivity, allowing pike and associated species to structure the fish community assemblage, and this may confound the classic concept. In addition, lakes below the highest postglacial coastline also allowed for historic colonizations of pike and associated fish community. Our results suggest that the first hierarchical filter (i.e., connectivity) is the fundamental basis rather than our second hierarchical filter (i.e., in-lake abiotic habitat: the "classic" concept) for the succession from nonsalmonid fish communities with pike to salmonid lakes. Well within the temperature ranges of salmonids and pike within these northern boreal regions, our results support this. Further support of this view is the evidence of highly eutrophic lakes that favour salmonids (e.g., Arctic char, brook trout, and brown trout) even at phosphorus levels >160 $\mu g \cdot L^{-1}$ (Näslund et al. 1993). This is provided that connectivity is sufficient to allow salmonids access to suitable reproductive areas and that pike and associated fish community are excluded by low connectivity. Compared with attempts to predict species composition on a landscape scale using our second hierarchical filter (including water quality), we suggest that both key piscivore presence (third filter) and its presence modelled indirectly through GIS data of connectivity (first filter) demonstrate the importance of key piscivore focused connectivity in determining the fish communities in boreal lakes. Our results imply that without pike, the fish community assemblages within this boreal landscape would shift towards resembling the salmonid-dominated landscape of lakes in, e.g., North American and European mountainous regions at the upper margins of pike habitat or even New Zealand, The Faroe Islands, and Iceland where pike have not (yet) colonized.

Future directions: improving standard characterization of lakes

We suggest that a shift of focus towards out-of-lake factors (first hierarchical filter: connectivity) and coexistence rules (third hierarchical filter) may facilitate understanding of the fundamental reasons why boreal lakes hold the fish communities they do. This may enable us to better understand the past, present, and potential diversity of lakes, understanding that is required for conservationists and fisheries managers to influence these ecosystems effectively towards a desirable future. We suggest that connectivity in drainage networks, described with migration barrier indicators like S_{Vsmax} or (and) more accurate field measurements of potential barriers, should be considered as standard characterization of lakes in fish community studies, just as pH and water depths are measured now. We do not suggest that variables like water chemistry are unimportant at lower levels, but in our large data set, connectivity provided much greater insight into the fundamental fish community (i.e., presence–absence) than water chemistry variables or lake morphometry, in spite of the large range of these variables among our lakes. Similarly, Amarasinghe and Welcomme (2002) showed that although chemical factors affect fish species richness in lakes, physical factors have greater predictive power worldwide. Mandrak (1995) analysed chemical and physical data from 10 167 Ontario lakes and concluded that species richness is not associated with lake chemistry or morphology when spatial autocorrelative effects are removed. Nash et al. (1999) criticized aquatic biologists for frequently being unaware of the pitfalls of spatial autocorrelation that lead to biased conclusions in ecological studies; in contrast, this is addressed by considering connectivity, which inherently causes patterns of spatially autocorrelated species distributions by contagious biotic processes (e.g., species spreading and replicating) between waters.

In closing, we first suggest that to conserve and manage freshwater fish species in drainage networks of lakes, it may be necessary to incorporate key piscivore focused connectivity. Secondly, our results show that piscivore-driven coexistence rules are a very strong third hierarchical filter that seals the fate of salmonid communities in most lakes. Overall, our collective evidence strongly implies that high pike-focused connectivity is the fundamental factor that explains why many of the coldwater, northern boreal lakes are not salmonid waters but dominated by fish such as perch, pike, roach, and other species more tolerant of pike predation.

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Mechanisms underlying the increase in young-of-the-year Atlantic salmon (*Salmo salar*) density with habitat complexity

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Abstract: We tested three hypotheses used to explain the increase in young-of-the-year (YOY) Atlantic salmon (*Salmo salar*) density with habitat complexity: the territory-size, predator-refuge, and foraging-benefits hypotheses. We manipulated habitat complexity in three different treatments (boulder-removed, control, and boulder-added) at eight sites in Catamaran Brook and the Little Southwest Miramichi River, New Brunswick. The density of juvenile salmon was two times higher in the boulder-added treatment than in the other treatments. Our data were consistent with the territory-size hypothesis; visual isolation was highest and territory size was smallest in the boulder-added treatment, and salmon selected microhabitats to maximize their field of view. Our results showed partial support for the predator-refuge hypothesis; salmon in the boulder-added sites were closer to cover and showed a reduced reaction distance to a novel stimulus, but did not preferentially select microhabitats closer to cover. We found no direct support for the foraging-benefits hypothesis; however, there is indirect evidence that boulders may improve the growth potential of instream habitat. Our results suggest that YOY Atlantic salmon may be attracted to complex environments for the increased cover and that the decreased visibility of these sites causes a reduction in territory size, allowing a higher density of fish.

Résumé : Nous vérifions trois hypothèses qui servent à expliquer l'augmentation de la densité de jeunes de l'année (YOY) en fonction de la complexité des habitats chez le saumon atlantique (*Salmo salar*), soit les hypothèses de la taille du territoire, des refuges contre les prédateurs et des avantages alimentaires. Nous avons manipulé la complexité des habitats par trois traitements expérimentaux (retrait de blocs rocheux, témoin, ajout de blocs rocheux) à huit sites dans Catamaran Brook et la rivière Little Southwest Miramichi, Nouveau-Brunswick. La densité de jeunes saumons était deux fois plus importante dans les sites d'ajout de blocs rocheux que dans les autres situations expérimentales. Nos données s'accordent avec l'hypothèse de la taille du territoire; l'isolement visuel est maximal et la taille des territoires minimale dans les conditions d'ajout de blocs et les saumons choisissent les microhabitats de façon à maximiser leur champ visuel. Nos résultats appuient en partie l'hypothèse des refuges contre les prédateurs; les saumons dans les sites d'ajout de blocs sont plus près d'un abri et ils ont une distance de réaction plus courte à un nouveau stimulus, mais ils ne choisissent pas leurs microhabitats préférentiellement en fonction de la proximité des abris. Nous ne trouvons aucun appui direct pour l'hypothèse des avantages alimentaires; il y a cependant des indications indirectes que les blocs rocheux peuvent améliorer le potentiel de croissance des habitats dans le cours d'eau. Nos résultats indiquent que les YOY du saumon atlantique peuvent être attirés par les habitats complexes pour un meilleur abri et que la visibilité réduite de ces sites entraîne une diminution de la taille des territoires, ce qui permet une plus grande densité de poissons.

[Traduit par la Rédaction]

Introduction

The structural complexity of a habitat has long been implicated as a major determinant of both species richness (MacArthur and MacArthur 1961) and the local abundance of particular species (Bell et al. 1991). Increases in the local density of fish species have been observed in a variety of ecosystems; lake piscivores increase with the abundance of submerged vegetation (Persson et al. 1991, 1992), reef fish density increases with coral complexity (Gorham and Alevizon 1989), and stream-dwelling salmonids increase with the abundance of coarse woody debris (Roni and Quinn 2001).

Habitat complexity is a particularly important habitat feature for stream-dwelling salmonids. Many models used to predict salmonid biomass (reviewed in Fausch et al. 1988) correlate fish abundance with measures of habitat complexity, such as the abundance of large woody debris or large-diameter substrates. Furthermore, the density of juvenile salmonid fishes often increases in response to habitat complexity, created by adding either boulders (Kalleberg 1958; Dolinsek et al. 2007*a*, 2007*b*) or artificial vegetation (Eklöv and Greenberg 1998). Three hypotheses are commonly invoked to explain the increase in salmonid density with habitat complexity: (*i*) the territory-size hypothesis, (*ii*) the predator-refuge hypothesis, and (*iii*) the foraging-benefits hypothesis (e.g., Fausch 1993; Culp et al. 1996; Imre et al. 2002).

The territory-size hypothesis assumes that visual isolation

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increases with habitat complexity (Kalleberg 1958). The increased visual isolation impedes the detection and expulsion of intruders (Eason and Stamps 1992) and the detection of food items (Wilzbach et al. 1986; Kemp et al. 2005), thereby leading to smaller territories in complex habitats (Kalleberg 1958; Imre et al. 2002) and higher densities of fish (Kalleberg 1958). Because of the increased costs of defence in low-visibility habitats, this hypothesis assumes that territorial fish do not prefer complex habitats (see Eason and Stamps 1992; Höjesjö et al. 2004). Hence, the territory-size hypothesis predicts an increase in density only when territory size limits the density of fish that can settle in a particular habitat.

In contrast, both the predator-refuge and the foraging-benefits hypotheses assume that complex environments are favorable microhabitats for settling fish. The predator-refuge hypothesis proposes that high-complexity habitats offer more cover from predators (Hartman 1965; Fausch 1993; Culp et al. 1996), so that fish near cover perceive a reduced risk of predation and therefore exhibit decreased wariness to predators, often quantified as the reactive distance to the approach of a predator or a novel stimulus (Ydenberg and Dill 1986; Grant and Noakes 1987). The foraging-benefits hypothesis proposes that an increase in habitat complexity leads to a greater variance in current velocity (see Crowder and Diplas 2000; Kemp et al. 2005), allowing fish to reduce their energy expenditure by holding position in low-velocity locations (Kalleberg 1958; Fausch 1984) while obtaining a foraging benefit from adjacent high-velocity locations that provide a drift-funneling effect (Huntingford et al. 1988; Mitchell et al. 1998).

Previous studies attempting to test these three hypotheses with stream salmonids have produced equivocal results for two reasons. First, most studies do not test all three hypotheses (e.g., Butler and Hawthorne 1968; DeVore and White 1978; Imre et al. 2002). Second, most studies assume that habitat complexity is only an attractive microhabitat feature (e.g., Fausch 1993) and ignore the possible negative consequences of reduced visibility (Eason and Stamps 1992; Höjesjö et al. 2004). Consequently, the relative importance of the three hypotheses in determining salmonid abundance remains unclear.

Here, we manipulated habitat complexity in a field study to test the predictions of the territory-size, predator-refuge, and foraging-benefits hypotheses. We first replicated Dolinsek et al. (2007*a*) to ensure that the density of juvenile Atlantic salmon (*Salmo salar*) increases with increasing habitat complexity. We then tested the specific predictions of each hypothesis (Table 1).

Materials and methods

Study area and study species

We collected data during July and August of 2004 in two streams in central New Brunswick, Canada (46°52′42″N, 66°06′00″W): the Little Southwest Miramichi River (fifth-order stream, mean width = 75 m) and one of its tributaries, Catamaran Brook (third-order stream, mean width = 7.2 m). We used eight study sites (mean area = 20 m^2, range = 17–23 m^2); three were located in a 60 m section of Catamaran Brook just upstream from its confluence with the Little Southwest Miramichi River. The remaining five sites were located in a 150 m section of the Little Southwest Miramichi River, just downstream from the mouth of Catamaran Brook. We selected sites that were deep enough for snorkeling observations, but were within the range of preferred habitats for young-of-the-year (YOY) Atlantic salmon in Catamaran Brook (Girard et al. 2004). For a general map of the study sites, see figure 1 in Steingrímsson and Grant (2003).

Of the six species of fish that are common at these particular sites in the two streams, Atlantic salmon are the most abundant (Dolinsek et al. 2007*a*). YOY Atlantic salmon emerge from the gravel by mid-June (Randall 1982) and typically spend three summers in the stream.

Experimental design

Following Dolinsek et al. (2007*a*), we manipulated habitat complexity using three different treatments (boulder-removed, control, and boulder-added) between 28 May and 1 June 2004, before the emergence of YOY salmon from the gravel in mid-June (Randall 1982). In the boulder-removed treatment, we removed all boulders and cobble greater than 10 cm along the longest axis (hereafter referred to simply as boulders). The control treatment was left undisturbed. In the boulder-added treatment, we removed all boulders and then added 48 boulders (mean diameter = 28 cm; range = 12–45 cm) in a uniform staggered design, similar to that used by Kalleberg (1958), for a mean boulder density of 6.5 boulders·m^{-2}. While there was variation among the control sections, they represented an intermediate level of complexity, which was generally more similar to the boulder-removed sections than to the boulder-added sections.

Each of the eight sites was divided into three equal quadrats (upstream, middle, and downstream), each measuring approximately 2 m long × 3.5 m wide. To ensure that the boulder-added and boulder-removed treatments had no effect on the control sites, the control treatment was always assigned to the most-upstream quadrat of the site. The boulder-added and boulder-removed treatments were randomly assigned to the middle and downstream quadrats of each site.

Density and size at age

Density estimates for all fish species were conducted during two daytime snorkeling surveys and one nighttime survey between 13 July and 16 July 2004. Daytime surveys were conducted between 1300 and 1800 h to coincide with the peak activity level of YOY Atlantic salmon in Catamaran Brook, whereas the nighttime survey was conducted between 2200 and 0200 h to coincide with the peak activity for ages 1+ and 2+ Atlantic salmon (Breau et al. 2007). For all surveys, a snorkeler moved slowly upstream, taking approximately 40 min to complete each of the eight sites. Fish were recognized as residing in the downstream, middle, or upstream quadrats based on the location of first sighting. For the nighttime survey, we used both a waterproof headlamp and a hand-held flashlight to illuminate fish, which were typically lethargic and unresponsive when approached. When conducting the density estimates, water levels were low in Catamaran Brook and some of the boulders in the

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Table 1. Predictions and results of the three hypotheses explaining the increase in Atlantic salmon (*Salmo salar*) density in high-complexity (boulder-added) habitats.

Hypothesis	Prediction: Fish in the boulder-added treatment...	Variable definition	Results[a]
Territory-size	have a reduced visual distance compared with fish in the other treatments	Visual distance: the average distance a fish can see before its vision is obstructed by an obstacle; measured in eight directions from the fish's primary foraging station	True
	defend smaller territories than fish in the other treatments	Territory size: the minimum area that encompasses 95% of a fish's aggressive acts, forging stations, and foraging attempts; mapped in ArcView GIS based on a 20 min underwater observation	True
	select microhabitats with a greater visual distance than randomly selected locations within the treatment	Visual distance: as above, except the fish's actual visual distance is compared with the visual distance of an imaginary fish at a paired, randomly-selected location within the same boulder-added section	True
Predator-refuge	are closer to cover than fish in the other treatments	Distance to cover: the distance between the fish's primary foraging station and the nearest location of possible cover	True
	"feel safer" and therefore show a reduced reactive distance to a simulated predator than fish in the other treatments	Reactive distance: the distance between the fish and an approaching novel stimulus when the fish takes flight	True
	select microhabitats that are closer to cover than randomly selected locations within the treatment	Distance to cover: as above, except the fish's actual distance to cover is compared with the distance to cover of an imaginary fish at a paired, randomly-selected location within the same boulder-added section	False
Foraging-benefits	experience a lower water velocity at their snout and a higher water velocity in their foraging zone	Snout velocity: current velocity measured at the fish's snout while at their primary foraging station; foraging velocity: current velocity at 40% depth at the fish's primary foraging station	False
	select microhabitats with a lower snout velocity and higher foraging velocity than randomly selected locations within the treatment	Snout and foraging velocity: as above, except measurements from actual fish are compared with that of an imaginary fish at a paired, randomly-selected location within the same boulder-added section	False
	have a higher foraging rate by taking advantage of faster velocities nearby	Foraging rate: the number of foraging attempts during a 20 min underwater observation	False
	have an increased growth rate	Growth rate: approximated by the average weight of fish in each treatment early and late in the growing season	False

[a]True means that results were consistent (i.e., $P < 0.05$) with the prediction; false means no significant effect.

boulder-added and control sections emerged above the water's surface. We did not include this reduction in usable habitat when calculating fish density, so any increases in density in these sites will be conservative.

We used mass at age as a measure of seasonal growth. To estimate mass, we used a field balance to weigh (±0.1 g) at least one YOY Atlantic salmon in each of the 24 quadrats early (17–18 July, $n = 53$) and late (30–31 August, $n = 55$) in the growing season. Beginning below a site, the snorkeler moved upstream and randomly selected a fish at the downstream end of the quadrat. If the fish appeared to hold a territory that extended outside of the quadrat or was behaving abnormally, another fish was selected. Each fish within the site that met the above criteria was sampled; however, as sampling progressed, the incidence of abnormal behaviour increased, presumably because of the disturbance of catching previous fish. Sampled fish were caught using two dipnets, and the location of the fish was marked by the placement of a numbered steel washer. Onshore, each fish was anesthetized in a separate bucket using clove oil (four drops per litre of water) and then weighed. Each fish was left to recover in a separate bucket of water for at least 10 min before being returned to its exact location of capture. When more than one fish was sampled in a treatment quadrat, we used the average mass as a datum in subsequent statistical analysis.

Territory size

We quantified the territory size of 37 YOY Atlantic salmon (hereafter referred to as focal fish) from 19 July to 1 August 2004 and from 16 August to 21 August 2004. We observed each focal fish for 20 min between 1300 and 1700 h. To conduct an observation, a snorkeler approached from downstream, randomly selected a focal fish and waited for 5 min before recording behaviour. While waiting, the observer sketched a map of the local streambed on a water-resistant Mylar sheet. During the observation, we mapped each foraging station (defined as any location where the fish maintained position for at least 5 s), recorded all switches between stations and the direction (1–12 o'clock, with 12 o'clock as directly upstream) and distance (in body lengths) of all foraging attempts and aggressive acts as well as the station from which they were initiated (see Steingrimsson and Grant 2008). In a foraging attempt, the fish begins at a foraging station and then darts up into the water column to intercept a food item, after which it returns di-

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rectly to the original foraging station. All foraging attempts were recorded regardless of whether the food item was intercepted, which was often difficult to determine. After each observation, we placed a numbered steel washer at the location of each foraging station.

At least one fish was observed in each quadrat, always starting with the downstream quadrat to minimize disturbance to future focal fish. To avoid observing the same fish twice, all observations within a given quadrat were completed without leaving the site. If a fish was lost from sight for more than 5 s, the observation was terminated. To reduce variation in other environmental variables, six of the eight sites were completed in a single day, and the remaining two sites were completed in two consecutive days.

To facilitate measurement, we placed a temporary wooden *x*–*y* grid on top of each territory in the stream. We measured the *x* and *y* location (±5 cm) of each foraging station in relation to the grid. These data were used to create a digital map using ArcView GIS 3.2 (ESRI, Redlands, California) with the Animal Movement extension (Hooge and Eichenlaub 2000). To estimate territory size, we first used the harmonic mean method (Hooge and Eichenlaub 2000) to remove spatial outliers (5%) and then applied the minimum convex polygon method (Schoener 1981) to the remaining 95% of all events (foraging stations, foraging attempts, and aggressive acts).

Microhabitat selection

During each territory observation, we recorded the distance above the substrate (±1 cm) and the direction (1–12 o'clock; ±30 min) of the focal fish's snout at its primary foraging station (i.e., the location from which most foraging attempts were initiated). All microhabitat measurements were taken at this location later that day. We measured snout velocity (see below), the average velocity of the water column, distance to cover, and visual distance (see below) at the primary foraging station of each focal fish (n = 37). For each focal fish in the boulder-added treatment (n = 14), we also measured these variables at a paired, randomly selected location within the same boulder-added quadrat, which was selected using randomly generated x and y coordinates.

We measured snout velocity, defined as the current velocity at the fish's snout, (±0.01 $m \cdot s^{-1}$) using a Marsh–McBirney meter (Model 201D, Fredericton, Maryland, USA). We measured average velocity of the water column at 40% of the depth from the water's surface, which is an approximation of the velocity regime experienced during foraging attempts. We quantified distance to cover (±1 cm) by stretching a marked string from the primary foraging station to the nearest location of possible cover, defined as any location on the substrate under which four fingertips could be hidden, approximating a suitable hiding place for juvenile salmon.

We measured visual distance (±1 cm), defined as the average distance a fish could see before its vision was obstructed, by holding one end of a string at the primary foraging station and stretching the other end out horizontally until it made contact with any obstruction. If no contact was made, we recorded a distance of 0.8 m, an estimate of the maximum foraging distance for a YOY salmonid fish (Dunbrack and Dill 1983). This procedure was repeated at 30° increments from –120° to +120°, with 0° being the direction the fish was facing. The average of these nine visual distances was used as an approximation of each focal fish's visual distance.

Perceived predation risk

To quantify perceived predation risk, we measured the reactive distance of 44 YOY Atlantic salmon to a novel stimulus (a fluorescent yellow ball of 4 cm in diameter attached to the end of a 2 m long metal rod of 1 cm in diameter) from 22 August to 24 August 2004. Reactive distance was measured in seven of eight sites; in the eighth site, no fish were observed in the boulder-removed treatment on the day of observation. To estimate reactive distance, we snorkelled upstream to the appropriate quadrat where we randomly selected an actively foraging fish. After waiting for 5 min to ensure the fish was foraging normally, we approached the focal fish from either 5 or 7 o'clock (with 12 o'clock as the direction the fish was facing) with the standard stimulus at a constant rate of 0.3 $m \cdot s^{-1}$; the stimulus was always visible to the fish during the approach. Reactive distance was defined as the distance (±0.5 cm) between the ball and the fish's snout at the time of flight. To avoid reobserving the same fish, all observations within a site were done without leaving the area.

Statistical analysis

Because of different patterns of diurnal activity (Breau et al. 2007), the density of YOY Atlantic salmon was calculated as the mean of the two daytime counts, whereas the density of ages 1+ and 2+ salmon was taken from the night count. Total salmon density was calculated as the sum of these two densities. While not reported, both YOY and parr density were also calculated as the mean of all three surveys and provided similar results to those reported here. Non-salmonid density was calculated as the mean density from all three surveys.

For most statistical tests, a datum in the analysis was the mean value for each of the eight quadrats of each treatment (n = 8). When comparing visual distance of focal fish against randomly selected locations in the boulder-added treatment, individual fish were considered as a datum (n = 14).

A one-way analysis of variance (ANOVA), using site as a block in a randomized block design, was used to test for differences in the dependent variables related to the a priori hypotheses (Table 1). A paired t test was used to compare the visual distance, distance to cover, snout velocity, and average velocity of focal fish against paired, randomly selected locations in the boulder-added quadrats.

Results

Density

The density of juvenile Atlantic salmon that were counted during snorkeling surveys was two times higher in the boulder-added treatment than in either the control or boulder-removed treatments ($F_{[2,14]}$ = 9.47, P = 0.003; Fig. 1). The increase in density in the boulder-added treatment was entirely due to an increase in the density of YOY Atlantic salmon ($F_{[2,14]}$ = 21.28, $P < 0.001$; Fig. 1); the den-

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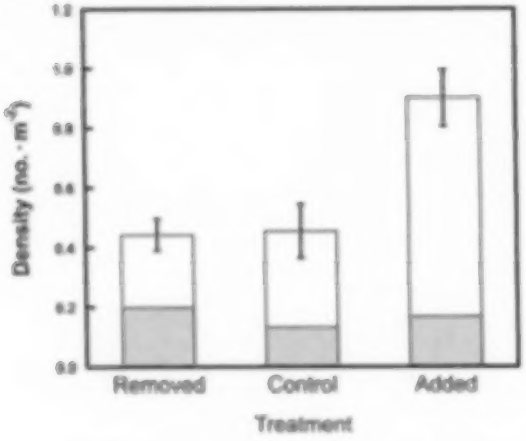
Fig. 1. Mean (±standard error, $n = 8$) density of juvenile Atlantic salmon (*Salmo salar*), separated into young of the year (open bars) and ages 1+ and 2+ (shaded bars), counted during three snorkelling surveys in the boulder-removed, control, and boulder-added treatments.



sity of Atlantic salmon parr (ages 1+ and 2+ fish) did not differ among treatments ($F_{[2,14]} = 0.76$, $P = 0.485$; Fig. 1). In addition, the combined density of all non-salmonid fishes (white sucker *Catostomus commersonii*, lake chub *Couesius plumbeus*, and eastern blacknose dace *Rhinichthys atratulus*) did not differ among treatments (not shown; $F_{[2,14]} = 0.99$, $P = 0.395$).

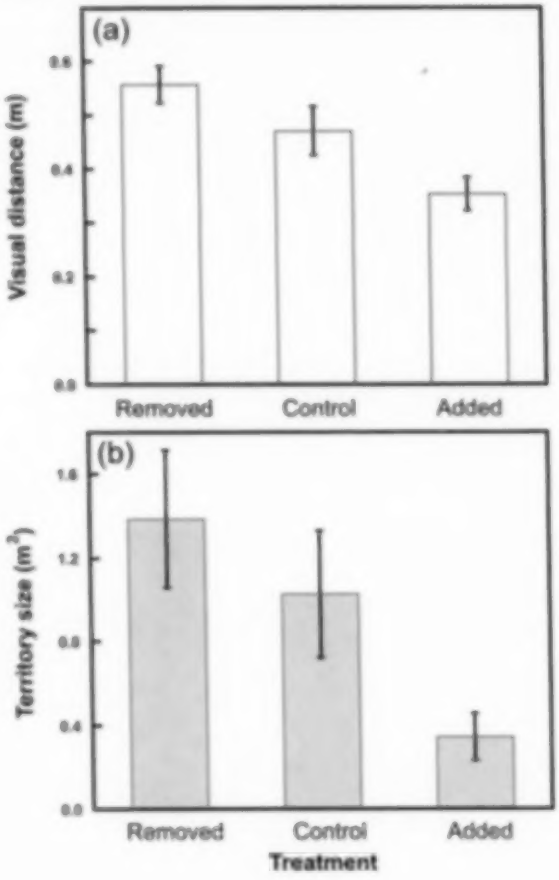
Territory-size hypothesis

Consistent with the territory-size hypothesis, the average visual distance for focal fish at their primary foraging station decreased with increasing habitat complexity ($F_{[2,14]} = 8.77$, $P = 0.003$; Fig. 2*a*). Furthermore, focal fish in the boulder-added quadrats selected primary foraging stations with a greater visual distance (mean ± standard error, SE = 35 ± 3.9 cm) than randomly selected locations (23 ± 2.6 cm) in the quadrat (paired t test: $t = 2.36$, df = 13, $P = 0.035$). Territory size based on the location of aggressive acts, foraging attempts, and foraging stations of focal fish also decreased significantly with increasing habitat complexity ($F_{[2,14]} = 4.28$, $P = 0.035$; Fig. 2*b*). On average, fish in the boulder-added treatment occupied a territory of 0.34 m^2 (±SE = 0.11) compared with 1.03 m^2 (±SE = 0.30) in the control treatment and 1.39 m^2 (±SE = 0.33) in the boulder-removed treatment. Despite the differences in territory size, the number of aggressive acts by focal fish did not differ significantly among the three treatments (mean ± SE acts·20 min^{-1} = 1.13 ± 0.37, 1.81 ± 0.44, and 1.63 ± 0.72 for boulder-removed, control, and boulder-added treatments, respectively; $F_{[2,14]} = 0.44$, $P = 0.655$). These results were consistent with the three predictions of the territory-size hypothesis (Table 1).

Predator-refuge hypothesis

As expected, the distance between the focal fish's primary foraging station and the closest suitable cover structure decreased with increasing habitat complexity ($F_{[2,14]} = 5.36$, $P = 0.019$; Fig. 3*a*). Within the boulder-added quadrats,

Fig. 2. Mean (±standard error, $n = 8$) (*a*) visual distance (distance between the fish's primary foraging station and a visual obstruction) and (*b*) territory size (95% minimum convex polygon) of young-of-the-year Atlantic salmon (*Salmo salar*) in the boulder-removed, control, and boulder-added treatments.



however, fish did not select foraging stations closer to cover (mean ± SE = 23 ± 3.6 cm) than randomly selected locations (18 ± 2.3 cm) (paired t test: $t = 2.14$, df = 7, $P = 0.07$). In fact, while the trend was not significant, focal fish in the boulder-added treatment tended to select primary stations that were further from cover than a random location in the quadrat. The reactive distance to the novel stimulus, our measure of perceived predation risk, decreased significantly with increasing habitat complexity ($F_{[2,12]} = 13.92$, $P = 0.001$; Fig. 3*b*). Our results were consistent with two of the three predictions of the predator-refuge hypothesis (Table 1).

Foraging-benefits hypothesis

Contrary to the foraging-benefits hypothesis, manipulating habitat complexity had no effect on the mean current velocity experienced at the snout of focal fish ($F_{[2,14]} = 0.293$, $P = 0.75$; Fig. 4) or in the water column above the fish ($F_{[2,14]} = 2.22$, $P = 0.146$; Fig. 4). Moreover, within the boulder-added treatment, focal fish selected microhabitats with snout velocities (mean ± SE = 0.160 ± 0.031 $m \cdot s^{-1}$)

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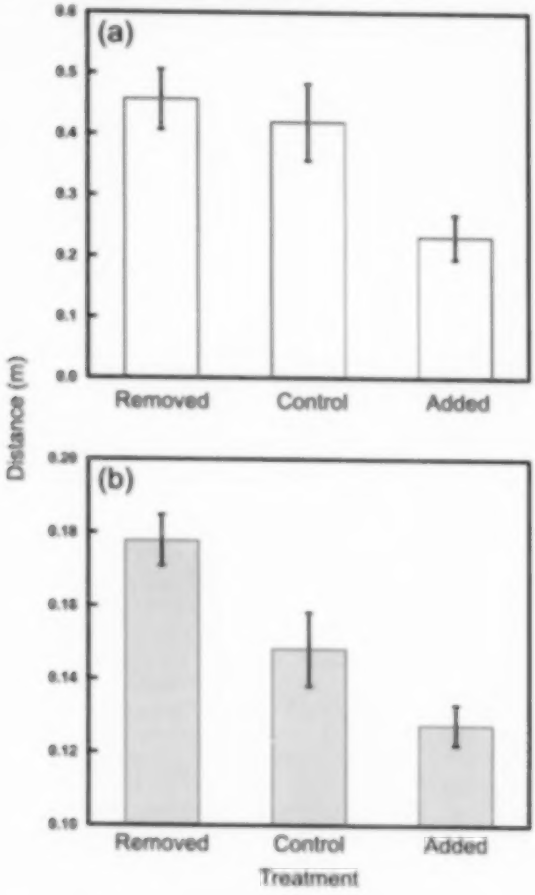
Fig. 3. Mean (±standard error) (*a*) distance to cover ($n = 8$) and (*b*) reactive distance to an approaching stimulus ($n = 7$) for young-of-the-year Atlantic salmon (*Salmo salar*) in the boulder-removed, control, and boulder-added treatments.



and water column velocities (0.363 ± 0.079 m·s^{-1}) that did not differ significantly from randomly selected locations (0.148 ± 0.029 m·s^{-1} and 0.319 ± 0.087 m·s^{-1}, respectively) within the quadrat (paired *t* test: $t = 0.27$, df = 7, $P = 0.798$; and $t = -0.82$, df = 7, $P = 0.437$, respectively).

Fish in the boulder-added treatment did not forage at a rate (mean ± SE = 3.15 ± 0.40 attempts·min^{-1}) that differed from fish in the boulder-removed (3.13 ± 0.37 attempts·min^{-1}) or control (2.88 ± 0.34 attempts·min^{-1}; $F_{[2,14]} = 0.30$, $P = 0.745$) treatments. Furthermore, our measure of growth rate, fish mass on either 17 July ($F_{[2,14]} = 1.05$, $P = 0.377$; Fig. 5) or 30 August ($F_{[2,14]} = 0.66$, $P = 0.535$; Fig. 5) did not differ significantly among the treatments.

Discussion

In our study, adding boulders to a stream increased the YOY Atlantic salmon density by 2 times, similar to the 2.0 or 2.8 times increases noted by others (Kalleberg 1958; Dolinsek et al. 2007*a*). Interestingly, adding boulders had no effect on the abundance of ages 1+ and 2+ Atlantic salmon parr. Our finding that older salmon did not respond to habitat complexity may be partially attributable to our sampling design, which only included one night observation. Using a more intensive sampling schedule, Dolinsek et al. (2007*a*) found that 1+ Atlantic salmon density did increase slightly with habitat complexity; however, the density of 2+ salmon did not differ significantly among treatments. Older salmon hold station higher off the substrate (Heggenes 1996), perhaps reducing any positive effects of adding boulders (see Kemp et al. 2005). In addition, because older salmon primarily feed at night (Breau et al. 2007), when the risk of predation is presumably reduced (Heggenes 1996), they may be less attracted by the cover provided by a complex habitat.

Our data demonstrate that using boulders to increase habitat complexity at least temporarily increases the density of YOY Atlantic salmon. Our experiment ran over a single

Fig. 4. Mean (±standard error, $n = 8$) current velocity at the snout of young-of-the-year Atlantic salmon (*Salmo salar*; open bars) and in the water column above the fish (shaded bars) in the boulder-removed, control, and boulder-added treatments.

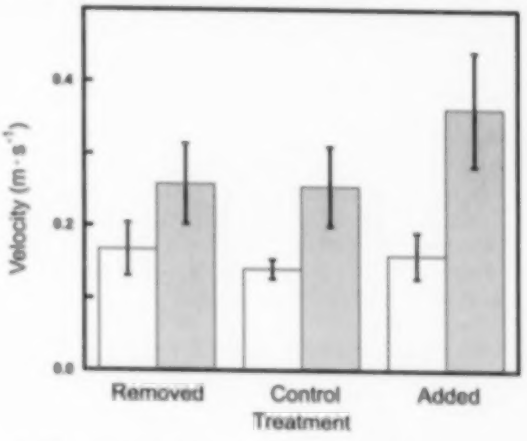
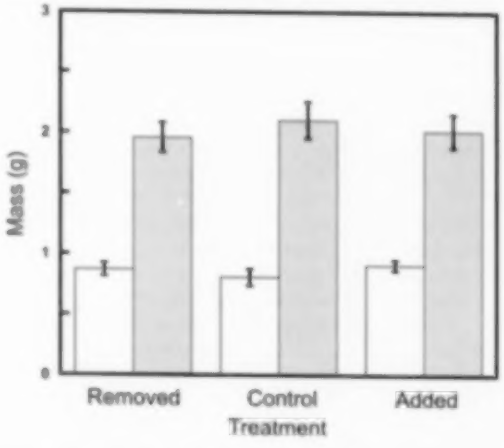


Fig. 5. Mean (±standard error, $n = 8$) body mass of young-of-the-year Atlantic salmon (*Salmo salar*) captured on 15 July (open bars) and on 28 August (shaded bars) 2004 in the boulder-removed, control, and boulder-added treatments.



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summer and density was estimated 4 weeks after emergence. Previous work, however, indicates that 73% of boulders remain within their original quadrat 1 year later and continue to have a positive effect on salmon density (Dolinsek et al. 2007*a*, 2007*b*). The long-term positive effects of adding boulders will likely be greatest in streams that are not subject to severe winter ice or spring spates, which serve to dislodge boulders. Moreover, the benefits to fish stock enhancement will be greatest if the density of older Atlantic salmon, which do not appear to benefit greatly from habitat complexity, is limited by YOY recruitment.

Similar to Dolinsek et al. (2007*a*), adding boulders had no significant effect on the density of non-salmonid fish. While not an a priori prediction, this result is consistent only with the territory-size hypothesis. The non-salmonids observed in this study are not territorial and therefore should not respond to increased visual isolation.

Our results support the territory-size hypothesis. YOY Atlantic salmon in the boulder-added treatment experienced a greater degree of visual isolation than YOY in the other treatments and apparently attempted to reduce this effect by selecting microhabitats with a greater field of view than at random sites. These data suggest that visual isolation may be a costly and undesirable habitat feature at the scale of a foraging territory. Moreover, fish in the complex habitat occupied smaller territories than fish in the other treatments.

To estimate whether the densities were sufficiently high that territoriality may have played a density-limiting role (sensu Fretwell and Lucas 1969), we calculated percent habitat saturation (PHS, sensu Grant and Kramer 1990) by multiplying the average density of fish by the average territory size in a quadrat. On average, 37% and 32% of the surface area of the boulder-removed and control treatments, respectively, were occupied by the territories of juvenile salmon. Both estimates are greater than a PHS of 27%, which was previously shown to result in space-related competition (Grant and Kramer 1990). Furthermore, these estimates of percent habitat saturation likely underestimate the actual degree of space competition, because not all habitat in each quadrat is usable, the boulders occupy some usable space, and only about 50% of juvenile salmon are visible at any one time in Catamaran Brook (Breau et al. 2007). Therefore, the densities and territory sizes in our study are consistent with the hypothesis that space competition may have limited population density in control and boulder-removed treatments.

Our results provided partial support for the predator-refuge hypothesis. Fish in the boulder-added treatment were closer to cover and had a shorter reactive distance to a standard stimulus than fish in the other two treatments. These results suggest that fish in complex habitat perceive themselves to be at a lower risk of predation. Juvenile brook trout (*Salvelinus fontinalis*) also show a positive relationship between distance to cover and reactive distance to a frightening stimulus (Grant and Noakes 1987). However, the predator-refuge hypothesis alone cannot explain our results. In the boulder-added treatment, fish did not select, and even seemed to avoid, positions close to cover. This result is consistent with the earlier finding from the territory-size hypothesis; fish in complex habitats apparently select foraging positions to maximize their field of view. Perhaps fish prefer sites with many hiding places, but within these safe sites select positions with good visibility to improve their vigilance towards predators, competitors, and prey items.

Our results did not support the foraging-benefits hypothesis. Fish in the boulder-added treatment did not experience or select for slower velocity microhabitats. Seeking refuge from high velocities may be less important for Atlantic salmon than for other salmonids, because they hold position against even strong currents by using their pectoral fins as hydrofoils against the substrate, rather than by actively swimming (Kalleberg 1958; Peake et al. 1997).

Contrary to the predictions of the foraging-benefits hypothesis, habitat complexity had no effect on the foraging rate of YOY Atlantic salmon. It was curious, however, that the density of salmon doubled in the boulder-added treatment with no apparent decrease in size-at-age, our measure of growth rate. Because fish were not individually tagged, we cannot be sure that captured fish spent the complete growing season within one quadrat. However, YOY salmon in Catamaran Brook are remarkably sedentary after settling, moving on average only 0.53 m in 8 weeks (Breau et al. 2007). Therefore, it is likely that most of the fish spent a considerable portion of the growing season in their quadrat of capture.

The lack of density-dependent growth in our experiment was initially surprising (Grant and Imre 2005), but may actually provide indirect support for the foraging-benefits hypothesis. The equal apparent growth rate among treatments and the higher densities in the boulder-added treatment are consistent with the ideal free distribution (Fretwell and Lucas 1969), as suggested by Girard et al. (2004) for Catamaran Brook, if the boulder-added treatment provided a better habitat for growth. Moreover, a recent study that controlled for fish density (Finstad et al. 2007) found that complex habitats did improve the growth potential of YOY Atlantic salmon during winter. Two possible mechanisms for an improved growth potential of complex habitat are (*i*) the funneling of water currents and drift by the boulders to create ideal foraging sites (Huntingford et al. 1988; Mitchell et al. 1998) or (*ii*) an increased production of benthos because of an increase in surface area of substrate or the increased retention of coarse particulate matter (Lepori et al. 2005; Storry et al. 2006). Alternatively, the increased cover in the boulder-added sites might reduce the maintenance metabolism of the fish because of lower stress levels (Millidine et al. 2006) and compensate for any density-dependent growth. The size-at-age data also suggest that the territory-size hypothesis alone cannot explain our results. If the decrease in habitat visibility caused by adding boulders is only a negative habitat feature, then growth rate should have decreased in the high-density boulder-added treatment.

In summary, our study suggests that the increase in YOY Atlantic salmon density caused by adding boulders cannot be fully explained by any single hypothesis. Our data support the idea that visual isolation in complex habitats reduces territory size, thereby facilitating higher fish densities. In addition, juvenile salmon are less wary to a novel stimulus, suggesting that boulders may be an attractive microhabitat feature. Finally, the absence of a reduction

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in growth in the high-density boulder-added treatment suggests that adding boulders improves the growth potential or carrying capacity of the habitat for juvenile salmon.

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Network models for ecosystem-based fishery analysis: a review of concepts and application to the Gulf of Alaska marine food web

Sarah K. Gaichas and Robert C. Francis

Abstract: We apply graph theory and network analysis to the food web of the Gulf of Alaska marine ecosystem to classify its structural properties, which suggest how the ecosystem as a whole may respond to heavy fishing pressure on its components. Three conceptual models of network structure, random, small-world, and scale-free, each have different implications for system behavior and tolerance to perturbations. We constructed two food web network models using detailed quantitative information on the stomach contents of 57 predator (fish) species collected during trawl surveys of the Gulf of Alaska between 1981 and 2002. The resulting food webs displayed both small-world and scale-free network properties, suggesting that impacts on one species might spread to many through short interaction chains and that while most food web connections are not critical, a small set of fished species support critical structural connections. Ecosystem-based fishery management should therefore first focus on protecting the highly connected species in the network to avoid structural impacts of fishing on the food web.

Résumé : Nous appliquons la théorie des graphes et l'analyse des réseaux au réseau alimentaire de l'écosystème marin du golfe de l'Alaska afin d'en classifier les propriétés structurales, ce qui laisse entrevoir de quelle manière l'écosystème dans son ensemble pourrait réagir à la forte pression de pêche exercée sur ses composantes. Trois modèles conceptuels de structure de réseaux, soit l'aléatoire, le petit monde et le modèle sans échelle, ont chacun des implications différentes sur le comportement du système et sa tolérance aux perturbations. Nous construisons deux modèles de réseau alimentaire à l'aide des renseignements quantitatifs sur les contenus stomacaux de 57 espèces de (poissons) prédateurs récoltés lors d'inventaires au chalut dans le golfe de l'Alaska entre 1981 et 2002. Les réseaux alimentaires obtenus possèdent des propriétés de réseau de type petit monde et sans échelle, ce qui indique que les impacts sur une espèce peuvent se transmettre à plusieurs autres à travers des courtes chaînes d'interaction et que, bien que la plupart des connections du réseau alimentaire ne soient pas critiques, un petit ensemble de poissons exploités sous-tend des connections structurales essentielles. Une gestion des pêches basée sur l'écosystème devrait se concentrer d'abord sur la protection des espèces fortement connectées dans le réseau, afin d'éviter les impacts structuraux de la pêche sur les réseaux alimentaires.

[Traduit par la Rédaction]

Introduction

Simple network models of complex food webs

Marine food webs can be extraordinarily complex, with thousands of species ranging from single-celled organisms to whales and humans connected by an intricate web of predator–prey interactions. Describing the structure of these food webs is challenging from both logistical and conceptual standpoints owing to data limitations, but this description is a basic requirement for ecosystem-based fishery management (Ecosystem Principles Advisory Panel 1999), because food web structure has implications for ecosystem function (e.g., Cury et al. 2000). Diverse disciplines ranging from computer and social sciences to epidemiology study how the structure (topology) of complex systems affects their function. In recent years, graph theory and network analytical concepts are providing valuable insights into system behavior in several of these fields (e.g., Hayes 1999; Strogatz 2001; Barabasi and Bonabeau 2003). Although systems such as living cells, the internet, and human social networks may at first appear unrelated to food webs, and network analyses are abstract compared with the more detailed biological studies typically conducted in fisheries research, there is evidence that model food webs with many of the complex attributes observed in nature can be constructed from surprisingly simple network properties (Williams and Martinez 2000). Recently, food webs have been increasingly modeled and analyzed as networks (e.g., Dunne et al. 2002;

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Williams et al. 2002; Garlaschelli et al. 2003) as have other ecological interactions, including parasitism, mutualism, and pollination (Montoya et al. 2006). Most simply, a marine or aquatic food web can be visualized as a network of predators connected to prey, but the properties of differently structured food web networks may imply different management strategies to sustain fisheries. Because graph theory and network analysis are not common tools in fisheries, we first review these concepts in abstract, then present an application of network analysis to the Gulf of Alaska (GOA) marine food web. We conclude by suggesting how network models and analyses might assist with ecosystem-based fishery management.

Graph theory and network analysis terminology

Graph theory originated with the work of Leonard Euler during the 18th century, when he solved the "Konigsberg bridge problem" of finding a path through a city crossing each of seven bridges only once by determining that no such path exists (Hayes 2000). The solution to the Konigsberg bridge problem modeled land adjacent to a bridge as a "vertex" or "node" and the bridges as "edges" or "links" joining the nodes. (In this paper, we adopt the network terminology used most commonly in computer science, where the entities in the network are called nodes and the connections between them are called links.) Once he defined the model, Euler calculated the "degree" of each node — the number of links meeting at the node. Euler discovered the network property that only a graph with two or fewer nodes of odd degree (odd numbers of links) contains a path where each link can be crossed just once. Since the four land nodes joined by the seven bridges all had odd degree, no path crossing all seven bridges only once existed in Konigsberg. Graph theory was applied to many different, relatively simple physical (circuits) and chemical (molecules) structures during the 19th century.

Because graph theory and network models arising from it have since been applied in diverse fields to a multitude of relationships, the terminology used to describe them is still evolving. In this review, we define key terms for the reader and proceed from simpler, historical models to more complex recent models of networks. Throughout the description, it is important to distinguish between the properties of the models and the properties of the "natural systems" they are intended to represent, which include food webs as well as other biological, physical, and social networks, and some networks of human origin, such as the internet. Network is a general term that applies to "any collection of units potentially interacting as a system" (Proulx et al. 2005, p. 346). The simplest model of a network is a graph with undirected links (e.g., predator and (or) prey interactions) between nodes (e.g., species in the food web), the structure we employ in all examples here. The simplest network model structure described by mathematicians and physicists is a regular lattice, which is characterized by perfect order with identical numbers and types of connections between components. The regular lattice network model clearly oversimplifies most natural systems described above, but it has some properties in common with them. Of the less ordered and more complex network models, three basic structural types have been described, each with different implications for system behavior and tolerance to perturbations. These network types include random networks, small-world networks, and scale-free networks (reviewed in Albert and Barabasi 2002 and Newman 2003). Each is described in detail below.

Random networks

Like the regular lattice, the random network model represents a mathematical extreme rarely observed in nature, but one with some properties useful for describing natural systems. Random network properties are derived from random graph theory, which was originally developed by Erdos and Renyi (1959, 1960, 1961), although it was also described by Solomonoff and Rapoport (1951; as reviewed in Albert and Barabasi 2002 and Newman 2003). Random graph theory is widely recognized to be one of the most important recent advances in the field of graph theory (Albert and Barabasi 2002; Newman 2003), because it provides statistical measures of system properties as graphs grow very large (i.e., in the limit as the number of nodes n approaches infinity). One of the pertinent properties of a random network is that any two nodes in the network have the same probability P of being connected (or probability $1 - P$ of not being connected). This probability of node connection determines the "degree distribution" of the network. For a small random network with few nodes, let $P = \lambda/n$, so the probability of a given node having degree k is given by the binomial distribution:

$$P(k \mid n, \lambda) = \left(\frac{n!}{k!\,(n-k)!}\right)\left(\frac{\lambda}{n}\right)^{k}\left(1-\frac{\lambda}{n}\right)^{n-k}$$

where λ is the average number of links per node, and n is the number of nodes. In the limit as n approaches infinity (i.e., for large networks), this becomes the Poisson distribution:

$$P(k \mid \lambda) = \frac{e^{-\lambda}\,\lambda^{k}}{k!}$$

Therefore, in large random networks, the connection probability P equals the average number of links per node λ using this notation.

Another important characteristic of random networks is the presence of "components" or "clusters" of nodes, which are joined together by shared links (Albert and Barabasi 2002; Newman 2003). In a random network with low connection probability P, many nodes may have no links to other nodes, and those that do form very small clusters of a few connected nodes. However, as P increases, Erdos and Renyi discovered a threshold where the random network rapidly changes from one with few small clusters to one with a "giant component" connecting most of the n nodes (Hayes 2000; Newman 2003). This threshold occurs where $P(n - 1) = 1$ (or $\lambda = 1$ in the above notation; Albert and Barabasi 2002; Newman 2003) or where the number of links equals the number of nodes. Above this threshold, the number of nodes in the giant component scales with n, the number of nodes in the entire random network, but the giant component has the property that its nodes are connected by relatively short path lengths (the number of links between a particular pair of nodes), which scale only as $\log n$ (Strogatz 2001). This property was first observed in natural systems

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within social networks (Milgram 1967) and is termed the "small-world effect" owing to the surprisingly close connection between any two nodes in the giant component. (In his famous experiment, Harvard psychologist Stanley Milgram asked randomly chosen people to get packages to an individual unknown to them and across the country by delivering the packages only to people they knew personally. He found that the packages arrived in an average of only six transfers between people (six links between nodes), which is the origin of the phrase "six degrees of separation.") Two related network statistics are "diameter" and "average path length." Diameter is the shortest path (in number of links) between the two most distant nodes in the network, or in other words, the longest direct path between two nodes. Average path length measures the average distance in links between any pair of nodes and scales with network diameter (Albert and Barabasi 2002).

Related to the concept of components or clusters is the clustering coefficient, C, which measures the tendency for members of a cluster to be fully connected to each other directly (rather than by several steps). There are several ways to calculate the C of a network (Newman 2003); here we use the definition given by Watts and Strogatz (1998) and the notation used in Albert and Barabasi (2002). Given a node i connected by its k_i links to k_i other nodes, the maximum number of links between the k_i other nodes if they are fully connected to each other is $k_i(k_i - 1)/2$. The clustering coefficient for the node i is the ratio between the actual number of links between the k_i nodes, E_i, and the maximum number of links possible:

$$C_i = \frac{2E_i}{k_i(k_i - 1)}$$

The clustering coefficient for the entire network is the average of the C_i values calculated at each node. Note that in a regular lattice, $C = 1$ because all nodes are connected to each other. In a random network, $C = P$ because links are distributed at random between nodes (Albert and Barabasi 2002; Newman 2003).

Until recently, random networks were the most useful model for representing complex networks that are clearly not well represented by a regular lattice (Albert and Barabasi 2002). While random networks with giant components have some properties observed in natural systems, such as the small-world property of relatively short average path lengths, other random network properties such as the Poisson degree distribution and relatively low clustering coefficients are generally not observed in a variety of natural systems (Albert and Barabasi 2002; Newman 2003).

Small-world networks

Small-world network models were developed by Watts and Strogatz (1998) to address some of the observed differences between the random network model and natural networks from social, physical, and biological systems. Given that many natural systems display both the regular lattice property of a high C and the random network property of short average path lengths between nodes (e.g., networks of actors connected by shared movies, a power grid network, and the neural network of *Caenorhabditis elegans*, a nematode worm), Watts and Strogatz (1998) derived an intermediate model with both properties by randomly rewiring some links of a regular ring lattice. This change connected formerly distant parts of the regular lattice, reducing overall average path length (called characteristic path length in Watts and Strogatz 1998) to that observed in a randomly connected network with the same number of nodes and links. In fact, the average path length in the small-world model was proportional to $\log n$, just as in the giant component of a random network. However, the introduction of some randomness in linkages did not eliminate the highly clustered property found in the original regular lattice, where neighboring nodes were generally fully connected to each other. Watts and Strogatz (1998) suggested that C measured a local property of the network, while the average path length measured a global property. In simulations where the original regular lattice links were randomly redirected with increasing probability, they discovered that average path length decreased rapidly, even at low "rewiring" probabilities, while C values remained uniformly high over a wider range of rewiring probabilities, suggesting that "the transition to a small world is almost undetectable at the local level" (Watts and Strogatz 1998). Another way to achieve the same network properties is to add shortcuts between randomly selected nodes in the regular lattice without disconnecting any original links (Newman 2003). While the combination of short average path lengths and large C values reflect properties of natural systems well, the degree distribution of the small-world network retains the characteristic shape from a random network of a Poisson distribution, in contrast with degree distributions observed in natural systems (Albert and Barabasi 2002; Newman 2003). Watts and Strogatz (1998) proposed that the small-world network structure implies certain dynamic properties related to the efficiency of information flow through the network: "enhanced signal-propagation speed, computational power, and synchronizability" relative to regular lattices.

Scale-free networks

Scale-free network models were developed by Barabasi and Albert (1999) to explain the observed "scale-free" or power law degree distributions observed in natural systems, which depart substantially from Poisson distributions. Scale-free in this context means network properties are independent of network size. Rather than starting with a fixed number of nodes and either linking them at random or rewiring existing regular lattice links (as in the random and small-world network models, respectively), Barabasi and Albert (1999) explicitly modeled the process of network development because they hypothesized that a particular process of network development leads to the observed degree distributions and other characteristics of natural systems. Two key assumptions underlie the process: first, networks start small and increase in size as new nodes are added; second, new nodes are not added at random, but with "preferential attachment" to the existing nodes of currently highest degree (Barabasi and Albert 1999; Albert and Barabasi 2002). The rationale for these assumptions is supported by observations from social and physical networks; for example, a network of scientific citations expands as new papers are published (nodes), and these new papers are more likely

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to cite (link to) papers that are already widely read and cited. (We will discuss whether this rationale applies to predator–prey relationships in food webs.) Modeling network development using these assumed processes, the observed degree distributions in model networks were strikingly similar to those observed in natural systems where $P(k)$ fit a power law, proportional to $k^{-\gamma}$ (Albert and Barabasi 2002; Barabasi and Bonabeau 2003; Newman 2003). In addition, the generated networks had structural features observed in natural systems, such as a handful of nodes acting as network "hubs" connecting many otherwise isolated nodes (Barabasi and Bonabeau 2003). Modeling the processes separately did not explain the power law degree distribution, so the authors concluded that both growth by node addition and preferential attachment of new nodes to existing nodes with probability proportional to the degree of existing nodes was required. Barabasi and Albert (1999) concluded that the success of this model in producing the observed power law degree distribution suggests "that large networks self-organize into a scale-free state, a feature unpredicted by all existing random network models."

In modeling processes leading to the power law degree distribution, scale-free network models also capture other observed properties of natural systems. Empirical results show that the scale-free network model's average path length is proportional to log n, similar to the giant component of a random network, but with even smaller average path lengths than similarly dimensioned random networks (Albert and Barabasi 2002). Therefore, the small-world property is observed in the scale-free network, but arises from a very different topology from that in the random network. In addition, clustering coefficients in scale-free models have intermediate properties between small-world networks, which maintain high clustering, and random networks, which have generally low clustering at large network size. As with average path length, there is currently no analytical solution for C in scale-free networks (Albert and Barabasi 2002).

The most important property of the scale-free network type, which shares key characteristics with natural systems, is the existence of a threshold between robustness and fragility, where a previously stable, connected structure may suddenly fragment under certain conditions. Albert et al. (2000) found that scale-free networks are generally robust to random failure (complete disconnection) of nodes, but are highly vulnerable to failure of the rare highly connected nodes. This error tolerance combined with attack susceptibility arises from the power law degree distribution; a randomly selected node from a scale-free network is highly likely to have very few links to other nodes. Therefore, removal of a node at random disconnects that node, but very few (if any) others from the network. Conversely, an attack directed at one of the high-degree nodes will remove that node and connections to a disproportionate number of other nodes, which may be connected to the network only through it. Therefore, the nodes formerly connected to the attacked high-degree node are highly likely to be disconnected from the network altogether. Albert et al. (2000) discussed the World Wide Web and social networks, while Solé and Montoya (2001) and Montoya and Solé (2002) extend the idea to food webs. They define the network structure of a food web with individual species at the nodes of the network and characterize the links between the nodes as predator–prey relationships — if one species eats another, their nodes are connected. In all analyses of these scale-free networks, the random removal of nodes (analogous to the extinction or local extirpation of a species) had little or no effect on the overall connectivity of the network, while a directed attack on highly connected nodes (or the loss of a highly connected species) resulted in the fragmentation of the network. Some pertinent questions for scale-free food web networks, then, are whether fishing on certain species constitutes a directed attack on the network, whether such an attack is likely to result in removal of a highly connected node, and what exactly network fragmentation means in a food web context.

Application

It seems reasonable to assume that if marine food web structure has implications for ecosystem function, then it also has important implications for fisheries management and conservation. The purpose of this network analysis is to examine system structure in the GOA food web, at least among the major fish species and their prey, using an original data set. The main goal is to classify the food web network according to its properties — is it a randomly connected network, a small-world network, a scale-free network, or some undescribed type? The properties of the network may imply how the system responds to heavy fishing pressure on its components.

Materials and methods

Previous studies of food web network properties have used food webs published by other workers (e.g., Camacho et al. 2002 used seven published food webs, which are a subset of the 16 published food web examined by Dunne et al. 2002). Therefore, information regarding how those food webs were constructed, what years of data they represented, and whether diets were based on stomach samples or other data was not available as part of the network analyses. Starting with an original data set, we describe both our food web construction methods and network analysis methods here.

The most comprehensive information available to determine some properties of the GOA food web comes from the food-habits database at the Alaska Fisheries Science Center (AFSC). The database contains detailed quantitative information on the stomach contents of 57 predator (fish) species collected during 18 surveys of the GOA between 1981 and 2002 (Table 1). Most fish were collected during summer months aboard standardized fishery-independent surveys using bottom trawls deployed at randomly selected locations within a depth- and latitude-stratified sampling frame. Complete survey methods for standard triennial trawl surveys (1984, 1987, 1990, 1993, 1996, 1999, and 2001) are detailed in Britt and Martin (2001). The sampling design for collecting fish stomachs aboard these surveys has varied somewhat over time, with certain species having different collection priority in different survey years (as evidenced by the variability in sample size by species between years in Table 1). Historically, collections were designed to sample a few common fish predators during every survey, and to ro-

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tate through secondary fish predators so that a complete set of species were collected over the course of two or three surveys. In 2001, this strategy was altered to collect from all common and secondary fish predators during each survey, so number of species collected increased but sample size for the common species decreased (see Table 1). The samples from nonstandard survey years included in the database represent opportunistic collections aboard special surveys or aboard fishing vessels, but in all cases the lab protocols for determining diets are the same. The diet data is derived from laboratory examination of the preserved stomachs with prey species recorded to the lowest possible taxonomic level. Over 450 species or species groups were recorded as prey in the database over the period 1981–2002.

We analyzed two different subsets of the data to determine whether sampling had any impact on conclusions about network type. First, collections from 1981 to 2000 were pooled so that each predator in the database was represented by the single annual collection resulting in the highest number of prey links for that predator. Then, any prey links that had been observed for that predator in other years that were not included in the selected year were added to the overall list of predator–prey links. Using these criteria, the sample years included for each predator ranged from 1985 to 2000, but with a concentration of links derived from 1990 to 1996 sampling (Table 2). This subset of the data reflected a food web constructed from multiyear collections rotating through different predators, which assumes a certain level of stability in predator feeding relationships across time, but also attempts to compensate for sampling errors in a given year, which resulted in links being missed. This first subset of data will be called the "multiyear food web" for the remainder of the paper. Second, we analyzed a single year's collection (2001) separately to reflect a food web constructed from a single year's snapshot of as many predators as possible. Recall that in 2001, the sampling strategy switched from annual rotation through a few highly sampled species to redistribute food habits sampling over a wider range of species. This second subset of data may have smaller sample sizes for any given predator than the first subset (so it may contain more errors of omission due to sampling effects), but no stability in diet over time is assumed in using a single year's collection. For the remainder of the paper, this second subset of data is called the "2001 food web."

In this analysis, we recorded only links between species; no information characterizing the strength or direction of the links was included; therefore our analysis is strictly topological, similar to previous studies (e.g., Dunne et al. 2002; Montoya and Solé 2002). The number of links per species was determined for all species in the network (not just predators but also prey) by calling something a link if one species had ever shown up in the other species' stomach. Identifying the direction of the links (prey to predator or vice versa) is straightforward, but not necessary for the analyses conducted here. Information on interaction strengths was purposely excluded from this analysis to focus on the purely topological network properties of the GOA food web.

We calculated the degree distribution for each food web network by summing the number of predator links and prey links for each species (node) and then compiling these results into a histogram showing the frequency of nodes having degree 1 through the maximum observed. For the multiyear food web, the degree distribution was calculated only using a single year's maximum prey and predator links for a given species groups (i.e., without the additional prey observed in other years listed in Table 2) so that it might be more comparable with the 2001 food web. Then the log frequency of nodes was regressed on the log degree to fit a linear function describing the exponent of the best power law fit to the data. Additional statistics calculated for each food web network included the diameter, average path length, and C value using the calculations described above. We visualized each network using the network analysis software Pajek (Slovene for "spider", available at vlado.fmf.uni-lj.si/pub/networks/pajek/), which also calculated the network statistics empirically from each network.

Because random networks have been used to represent the default model for natural system networks (Albert and Barabasi 2002), we constructed two random networks with the same number of nodes and links as the GOA multiyear and 2001 food web networks using Pajek. (The software automatically generates a random network given the number of nodes and links.) The diameter, average path length, and C values were calculated for the two random networks and compared with the results for the GOA multiyear and 2001 food web networks.

Results

The GOA multiyear food web has visual features strongly resembling those of scale-free networks, with at least four network "hubs" appearing as nodes connecting to unique clusters of nodes as well as to the main network (Fig. 1*a*). This visual structure contrasts strongly with that of a random network constructed with the same number of nodes and links as the multiyear food web (Fig. 1*b*). The results were visually similar between the multiyear food web and the 2001 food web, which also displays the characteristic hubs of a scale-free network, although there are only three obvious hubs in this view (Fig. 2*a*). As with the multiyear food web, comparison of the 2001 food web network and a random network with the same number of nodes and edges shows little visual similarity to the 2001 food web (Fig. 2*b*).

Statistical analysis of network properties indicates that the GOA food web networks constructed from this database display aspects of both small-world and scale-free network properties, regardless of the years included in the analysis. In the first analysis using aggregated multiyear collections from 1987 to 2000, there were 406 nodes and 1057 links included in the food web network, so that on average one could expect 2.6 links per node. The diameter of the multiyear food web network (the minimum path between the two most distant nodes) was only five links (Table 3). Average path length for this multiyear food web network was 2.6 links. In contrast, the diameter of an equivalent random network with 406 nodes and 1057 links was 14, and the average path length was 5.9, implying that the food web network had a stronger small-world effect than the random network. The 2001 food web displayed similar properties to the multiyear food web. Using only collections from 2001, there were

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Table 1. Number of stomachs collected for each predator and year in the Gulf of Alaska food habits database, 1981–2002.

	Year							
Predator	1981	1984	1985	1986	1987	1990	1991	1992
Albatrossia pectoralis (giant grenadier)					8			
Anoplopoma fimbria (sablefish)					108	335		22
Aptocyclus ventricosus (smooth lumpsucker)				24				
Atheresthes evermanni (Kamchatka flounder)					1			
Atheresthes stomias (arrowtooth flounder)			4	15	134	1 143	45	43
Bathymaster signatus (searcher)								
Bathyraja interrupta (sandpaper skate)								
Bathyraja parmifera (Alaska skate)								
Coryphaenoides acrolepis (Pacific grenadier)								
Dasycottus setiger (spinyhead sculpin)								
Embassichthys bathybius (deepsea sole)								
Gadus macrocephalus (Pacific cod)	241	96	57	10	131	932	90	29
Glyptocephalus zachirus (rex sole)					28			
Hemilepidotus jordani (yellow Irish lord)					8			
Hemitripterus bolini (bigmouth sculpin)								
Hippoglossoides elassodon (flathead sole)			60		62		13	
Hippoglossus stenolepis (Pacific halibut)						467		15
Isopsetta isolepis (butter sole)								
Lepidopsetta bilineata (rock sole)								
Lepidopsetta polyxystra (northern rock sole)								
Lepidopsetta sp. (rock sole type)			5	17	25			
Leptocottus armatus (Pacific staghorn sculpin)								
Limanda aspera (yellowfin sole)			13					
Liparis gibbus (variegated snailfish)								
Lampenella longirostris (longsnout prickleback)								
Lycodes brevipes (shortfin eelpout)								
Lycodes diapterus (black eelpout)								
Lycodes palearis (wattled eelpout)								
Malacocottus zonurus (darkfin sculpin)								
Mallotus villosus (capelin)								
Microstomus pacificus (Dover sole)					43			
Myoxocephalus polyacanthocephalus (great sculpin)								
Oncorhynchus keta (chum salmon)								
Oncorhynchus tshawytscha (Chinook salmon)				23				8
Pleurogrammus monopterygius (Atka mackerel)					8			
Pleuronectes quadrituberculatus (Alaska plaice)								
Podothecus accipenserinus (sturgeon poacher)								
Raja binoculata (big skate)								
Reinhardtius hippoglossoides (northern rock sole)								
Sebastes alascanus (rougheye rockfish)					41	153		10
Sebastes alutus (Pacific ocean perch)	201			30	23	147		
Sebastes babcocki (redbanded rockfish)								
Sebastes borealis (shortraker rockfish)					22	10		
Sebastes ciliatus (dusky rockfish)					16	41		3
Sebastes maliger (quillback rockfish)								
Sebastes pinniger (canary rockfish)								
Sebastes polyspinis (northern rockfish)					51	57		
Sebastes ruberrimus (yelloweye rockfish)					2			
Sebastes variegatus (harlequin rockfish)					5			
Sebastes zacentrus (sharpchin rockfish)								
Sebastolobus alascanus (shortspine thornyhead)					12	136		
Somniosus pacificus (Pacific sleeper shark)								
Squalus acanthias (spiny dogfish)								
Thaleichthys pacificus (eulachon)								
Theragra chalcogramma (walleye pollock)			64	179	125	1 122	157	115
Trichodon trichodon (Pacific sandfish)								
Zaprora silenus (prowfish)								
Total	442	96	203	298	853	4 543	305	245

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1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	Total
								25		33
431		51	100	67	30	165	74	464		1847
										24
										1
2085	137	210	2244	39	464	1506	7	2218		10294
								11		11
								4		4
								2		2
								1		1
								25		25
								3		3
1082	14	202	614	27	539	900	5	1143		6112
								81		109
								3		11
						3		4		7
692					152	293		58		1330
559			367	9	78	388	27	992		2902
								19		19
			120			165		33		318
			136			135		32		303
										47
								1		1
						60		2		75
								1		1
								7		7
								4		4
								1		1
								3		3
								17		17
								1	337	338
								54		97
								6		6
								2		2
								1		32
			42			31		30		111
								3		3
								1		1
								2		2
								1		1
279								36		519
								57		458
								4		4
20						41		46		139
								14		74
							11			11
							1			1
								1		109
							5	17		24
										5
52						6		18		76
213								41		402
			13							13
								1		1
								54		54
1195	1103	997	938	65	414	1117	594	1069	518	9772
								2		2
			18							18
6608	1254	1460	4592	207	1677	4810	724	6615	855	35787

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Table 2. Sample years included in construction of the multiyear Gulf of Alaska food web network model for each predator.

Year	Collected predator species	No. of links	Additional prey links	Additional prey collection years
1985	*Limanda aspera* (yellowfin sole)	6		
1986	*Aptocyclus ventricosus* (smooth lumpsucker)	5		
1986	*Oncorhynchus tshawytscha* (Chinook salmon)	6		
1987	*Atheresthes evermanni* (Kamchatka flounder)	1		
1987	*Albatrossia pectoralis* (giant grenadier)	4		
1987	*Glyptocephalus zachirus* (rex sole)	13		
1987	*Hemilepidotus jordani* (yellow Irish lord)	6		
1987	*Lepidopsetta* sp. (rock sole type)	9		
1987	*Microstomus pacificus* (Dover sole)	15		
1987	*Sebastes borealis* (shortraker rockfish)	6		
1987	*Sebastes ruberrimus* (yelloweye rockfish)	2		
1987	*Sebastes variegatus* (harlequin rockfish)	3		
1990	*Anoplopoma fimbria* (sablefish)	58	6	1987, 1993, 1998
1990	*Gadus macrocephalus* (Pacific cod)	166	45	1984, 1987, 1993, 1995, 1996, 1999
1990	*Hippoglossus stenolepis* (Pacific halibut)	115	21	1993, 1996, 1999
1990	*Sebastes aleutianus* (rougheye rockfish)	42		
1990	*Sebastes alutus* (Pacific ocean perch)	37		
1990	*Sebastes ciliatus* (dusky rockfish)	20		
1990	*Sebastes polyspinis* (northern rockfish)	17		
1990	*Sebastolobus alascanus* (shortspine thornyhead)	45	1	1993
1990	*Theragra chalcogramma* (walleye pollock)	110	15	1993, 1995, 1996, 1998, 1999
1993	*Sebastes zacentrus* (sharpchin rockfish)	9		
1996	*Atheresthes stomias* (arrowtooth flounder)	72	14	1990, 1993, 1998, 1999
1996	*Lepidopsetta bilineata* (rock sole)	40	1	1999
1996	*Lepidopsetta polyxystra* (northern rock sole)	48	1	1999
1996	*Pleurogrammus monopterygius* (Atka mackerel)	12	1	1987
1996	*Somniosus pacificus* (Pacific sleeper shark)	17		
1996	*Zaprora silenus* (prowfish)	7		
1998	*Hippoglossoides elassodon* (flathead sole)	44	5	1987, 1993, 1999
1999	*Hemitripterus bolini* (bigmouth sculpin)	1		
2000	*Sebastes maliger* (quillback rockfish)	10		
2000	*Sebastes pinniger* (canary rockfish)	1		
Total		947	110	

Note: Year denotes the primary year's data used to describe the majority of links (predators and prey) for the collected predator species. The number of predator and prey links identified in the primary year is given in the number of links column. Additional prey links refers to the number of prey links identified for the collected predator species in years other than the primary year, which were added to ensure complete sampling. Additional prey collection years lists all years where the unique additional prey of the collected predator species were observed in the database.

307 nodes and 1011 links, for an average of 3.3 links per node. Similar to the multiyear food web, the diameter of the 2001 food web network was 6, and the average path length was 2.6. The diameter of the corresponding random network shown in Fig. 2*b* is 11, and the average path length of that network was 4.7, again suggesting a stronger small-world effect in terms of path length in the 2001 food web network than in an equivalent random network.

The degree distributions of both the multiyear and the 2001 food webs are most similar to that of the scale-free network (Figs. 3 and 4). In both cases, the frequency distribution of the number of links per species (node) fits a power law well. For the multiyear food web, a linear regression on log-transformed data estimated an exponent of 0.9689 with $R^2 = 0.89$ (Fig. 3, lower panel), indicating that this is a scale-free network. Results were similar for the 2001 food web, where the estimated exponent was 0.9782 with $R^2 = 0.79$ (Fig. 4, lower panel).

Average C values for each network did not suggest greatly different structure between the two data sets or between the food web networks and the random networks. The 2001 GOA network and the random network with the same node and link counts had higher average C values than the multiyear food web and its corresponding random network, perhaps because the 2001 networks had relatively fewer nodes for a similar number of links (Table 3). While the average C was higher for the food web networks than the random networks, the differences were small. However, comparison of the distributions of C reveals substantial differences; food web networks have a handful of nodes with high clustering and many with very low clustering, while random networks have many nodes with an intermediate level of clustering (Table 4). The effect is dramatic. The top four species' nodes in the food web networks had clustering coefficients an order of magnitude higher than those calculated for the top four nodes in random networks; by

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Fig. 1. (*a*) Multiyear food web constructed from the Gulf of Alaska (GOA) food habits database, where each species is a node (dots) and each predator–prey interaction is a link (lines). (*b*) Random network constructed with the same number of nodes (406) and links (1057) as the GOA multiyear food web. Figures are 3D projections; node size is equal but the projection makes farther nodes appear smaller.

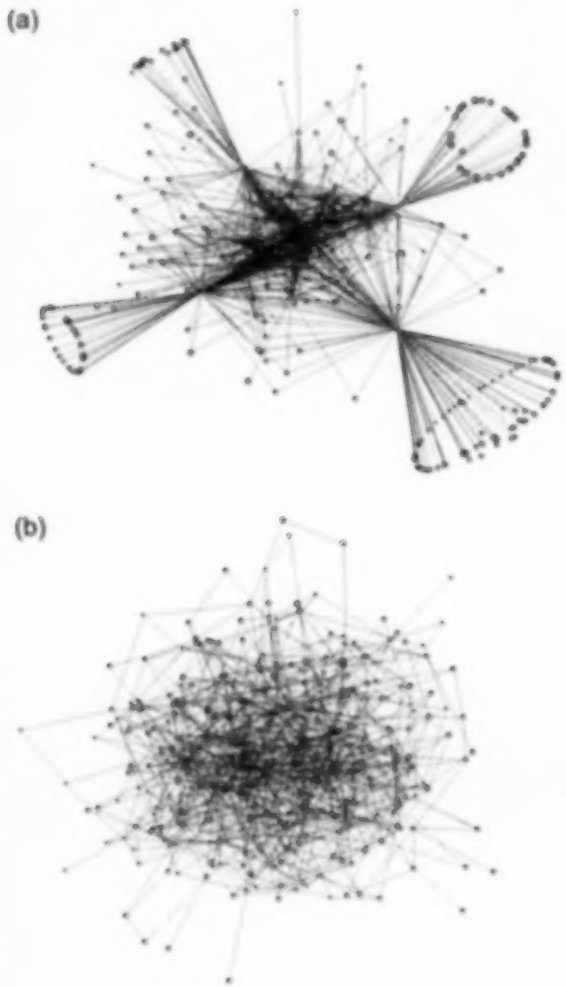
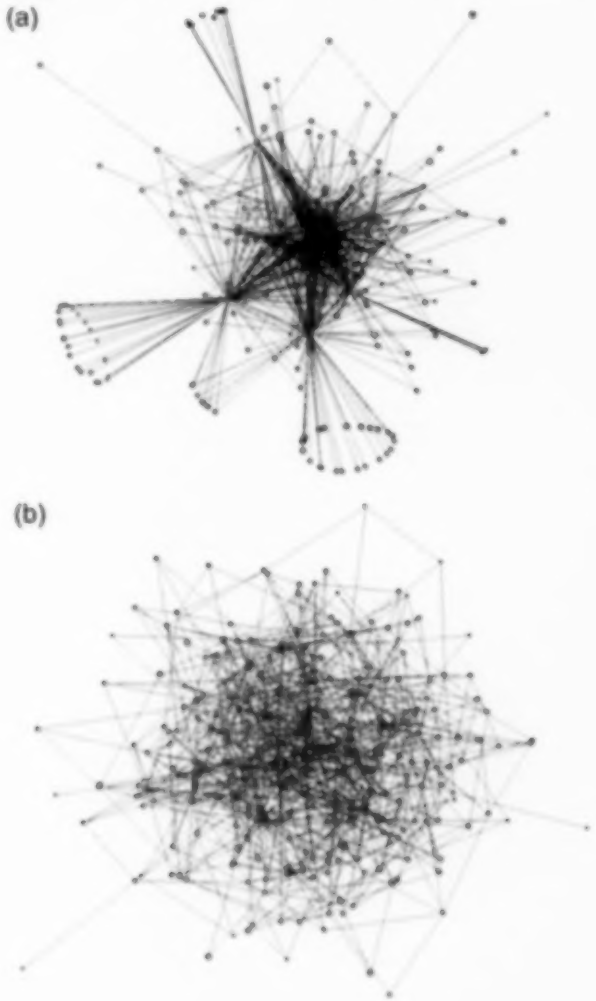


Fig. 2. (*a*) 2001 food web constructed from the Gulf of Alaska (GOA) food habits database, where each species is a node (dots) and each predator–prey interaction is a link (lines). (*b*) Random network constructed with the same number of nodes (307) and links (1011) as the GOA 2001 food web. Figures are 3D projections; node size is equal but the projection makes farther nodes appear smaller.



the 20th-ranked node, the food web C values were an order of magnitude lower than the correspondingly ranked nodes in random networks. The species with the highest C in both the multiyear and the 2001 GOA food web networks was Pacific cod (*Gadus macrocephalus*), with nearly identical values around 0.42 in both networks (Table 4). Pacific halibut (*Hippoglossus stenolepis*) and walleye pollock (*Theragra chalcogramma*) had the next highest clustering coefficients in each food web. Pollock had higher clustering than halibut in the multiyear food web, a situation which reversed in the 2001 food web. Arrowtooth flounder (*Atheresthes stomias*) rounded out the top four nodes in both food web networks.

The average C values observed in the real food webs are heavily influenced by the hub species with the most links in each network. The most highly connected species in the multiyear food web network were Pacific cod (169 links), Pacific halibut (118 links), walleye pollock (117 links), and arrowtooth flounder (78 links; Table 5). Considering that the food webs were assembled from independent data sets, these results are strikingly similar to those found in the 2001 food web network, where the highly connected species were also Pacific cod (161 links), Pacific halibut (143 links), walleye pollock (91 links), and arrowtooth flounder (91 links; Table 6). The rank order of links and C is identical in the 2001 food web model, but in the multiyear model, walleye

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Table 3. Summary of network statistics comparing the multiyear Gulf of Alaska (GOA) food web network, a random network with multiyear node and link numbers (Random 1), the 2001 GOA food web network, and a random network with 2001 node and link numbers (Random 2).

Statistic	Multiyear GOA food web	Random 1	2001 GOA food web	Random 2
No. of nodes	406	406	307	307
No. of links (undirected)	1057	1057	1011	1011
Average links per species	2.60	2.60	3.29	3.29
Diameter (of connected component)	5	14	6	11
Average path length	2.59	5.91	2.63	4.72
Average clustering coefficient (C)	0.00261	0.00224	0.00416	0.00298

pollock, a node with one less link than Pacific halibut, has a higher C (Table 4).

Discussion

Viewing the GOA food web from the perspective of network theory provides new insights into system structure and behavior of potential importance for fishery management. The GOA food web networks constructed from this database display several of the small-world and scale-free properties found in other complex networks (Watts and Strogatz 1998; Barabasi and Albert 1999; Barabasi and Bonabeau 2003). It is important to note that these complex network properties emerge regardless of the analytical approach used to construct the food web by sampling the database over multiple years or within a single year. In this section, we first address whether the observed network characteristics might still arise from the data collection methods rather than the GOA marine ecosystem itself and suggest what alternative analyses might be performed to validate or refute these results. Second, we compare the present results with those found in other food web network studies to determine whether the GOA has similar properties. Third, we suggest network-formation processes other than "preferential attachment", which might result in a scale-free network structure in food webs. Finally, we explore the management implications of fishing in a food web that exhibits scale-free and small-world network properties.

Sampling-driven network structure?

While these results clearly indicate a scale-free network structure in food webs constructed from the AFSC food habits database, it is important to ensure that the observed structure does not arise exclusively from the design of the food habits sampling program and the database itself (a topic not addressed in previous studies based on published food webs). Because this database was constructed specifically to examine the food habits of the fish that are major predators in the system, it contains no information on the food habits of their numerous invertebrate and planktivorous prey. This focus on fish predators may create the power law degree distribution simply through sample bias, so that predator species are highly connected while prey species are less so, and numerous rare prey in the diets of certain predators can have only one link back to the predator itself. Further, in the multiyear food web, the most highly connected species (Pacific cod, walleye pollock, Pacific halibut, and arrowtooth flounder) are also the most intensively sampled across years in this database. In theory, the process of repeatedly sampling these four species year after year could also result in a scale-free distribution — new links are preferentially added to these nodes because they are preferentially sampled. However, we avoided this particular bias by including the maximum number of links from a single sampling year in the degree distribution, not the sum of all links for a given species in the database. While the database does show that these four species have varied diets with at least this many connections to prey, it is possible that some less intensively sampled species might also have high connectivity that we have failed to detect because it was poorly represented in the database. Indeed, some predators are represented by very few stomach samples in any collection year, thus limiting the potential number of prey observed for them. Finally, these predator fish species are almost all also the prey of animals at higher trophic levels, including Steller sea lions (*Eumetopias jubatus*), killer whales (*Orcinus orca*), and some sharks which have not been included in this database. Some additional links in the food web can be derived from existing information in marine mammal food habits databases and other literature, while other links may only be found through additional field sampling of prey species as well as predator species.

While more thorough sampling could clarify linkages and perhaps identify other well-connected species, the fact that a single year's collection in 2001 designed to sample as many predators as possible has the same characteristics as the multiyear web argues in favor of the scale-free degree distribution arising from the food web itself and not from selective sampling. Further, the addition of more predators of groundfish and the prey of groundfish prey would be likely to increase the number of nodes and links and perhaps the mean links per node, but it is not clear that the power law degree distribution would change substantially. Partial evidence is provided by comparing the multiyear and 2001 food webs themselves; the multiyear food web was designed to compensate for annual sampling constraints and have as many predators as possible, while the 2001 food web was constrained by a single year's sampling and had 100 fewer predators than the multiyear food web. Nevertheless, the webs have nearly identical structural characteristics (incidentally suggesting also that food web structure has been relatively stable over the time period represented). A

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Fig. 3. Degree distribution for the multiyear Gulf of Alaska food web; points indicate frequency of nodes with degree k, and the line indicates fit to a power law. Inset: Same information on a log scale, with linear equation and line describing the fit of a power law to points indicating log frequency of nodes with degree log (k).

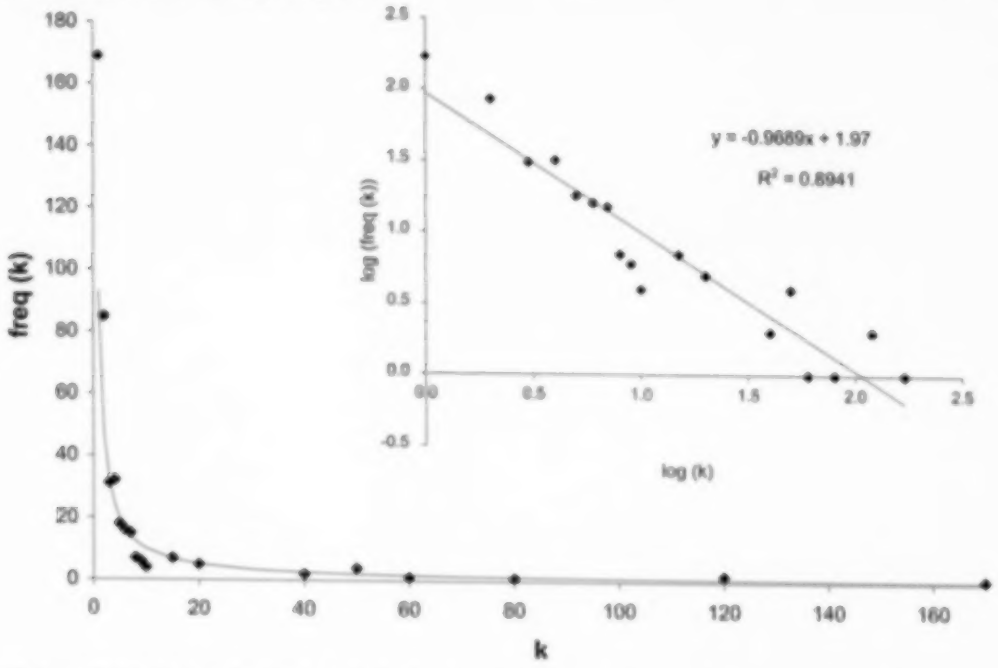

Fig. 4. Degree distribution for the 2001 Gulf of Alaska food web; points indicate frequency of nodes with degree k, and the line indicates fit to a power law. Inset: Same information on a log scale, with linear equation and line describing the fit of a power law to points indicating log frequency of nodes with degree log (k).

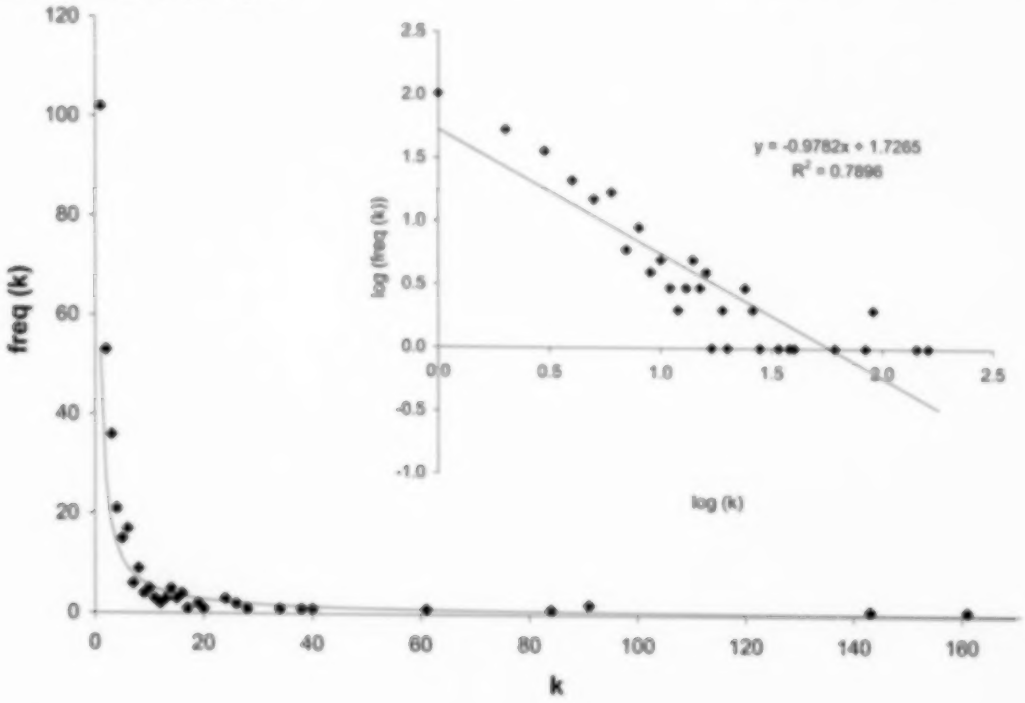

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Table 4. Top 20 clustering coefficients (C) measured for individual nodes from the multiyear Gulf of Alaska (GOA) food web network, a random network with multiyear node and link numbers (Random web 1), the 2001 GOA food web network, and a random network with 2001 node and link numbers (Random web 2).

Multiyear GOA food web node (top 20)	C	Random web 1 node	C	2001 GOA food web node (top 20)	C	Random web 2 node	C
Gadus macrocephalus (Pacific cod)	0.421053	v203	0.030769	*Gadus macrocephalus* (Pacific cod)	0.4222503	v140	0.024855
Theragra chalcogramma (walleye pollock)	0.202253	v342	0.030769	*Hippoglossus stenolepis* (Pacific halibut)	0.3045833	v91	0.0232964
Hippoglossus stenolepis (Pacific halibut)	0.169429	v103	0.029777	*Theragra chalcogramma* (walleye pollock)	0.1706392	v83	0.0213904
Atheresthes stomias (arrowtooth flounder)	0.105625	v393	0.029586	*Atheresthes stomias* (arrowtooth flounder)	0.1480872	v250	0.0203046
Anoplopoma fimbria (sablefish)	0.043806	v70	0.028623	*Anoplopoma fimbria* (sablefish)	0.1164606	v143	0.0200535
Hippoglossoides elassodon (flathead sole)	0.029364	v93	0.026125	*Sebastolobus alascanus* (shortspine thornyhead)	0.0144782	v278	0.020025
Sebastolobus alascanus (shortspine thornyhead)	0.018254	v113	0.024292	*Dasycottus setiger* (spinyhead sculpin)	0.0090531	v178	0.0193687
Lepidopsetta bilineata (rock sole)	0.009833	v100	0.023932	*Hippoglossoides elassodon* (flathead sole)	0.0081907	v16	0.0179028
Sebastes alutus (Pacific ocean perch)	0.009178	v235	0.023222	*Thaleichthys pacificus* (eulachon)	0.0065315	v217	0.0142315
Somniosus pacificus (Pacific sleeper shark)	0.003196	v88	0.022514	*Sebastes alutus* (Pacific ocean perch)	0.0063832	v119	0.0138655
Caridea (shrimp)	0.002665	v43	0.022333	*Lepidopsetta bilineata* (rock sole)	0.0047977	v220	0.0135747
Polychaeta (worm)	0.002236	v66	0.021978	Gammaridea (amphipod)	0.0033506	v269	0.0135747
Osteichthyes: Teleostei (fish)	0.002041	v201	0.021978	Osteichthyes: Teleostei (fish)	0.0026079	v174	0.0130719
Microstomus pacificus (Dover sole)	0.002011	v360	0.021669	Polychaeta (worm)	0.0025918	v149	0.012735
Crangonidae (shrimp)	0.001803	v147	0.021368	Amphipoda: Hyperiidea (amphipod)	0.0024248	v75	0.0124567
Paguridae (hermit crab)	0.001729	v376	0.021368	*Thysanoessa inermis* (euphausiid)	0.002065	v93	0.0124434
Gammaridea (amphipod)	0.00166	v144	0.02122	Pandalidae (shrimp)	0.0020156	v244	0.0123839
Sebastes polyspinis (northern rockfish)	0.001599	v205	0.019231	Caridea (shrimp)	0.0019484	v84	0.0120321
Lepidopsetta sp. (rock sole type)	0.001594	v274	0.019231	Euphausiacea (euphausiid)	0.0018537	v287	0.0116354
Bivalvia (clam)	0.001286	v333	0.017752	Mysidacea: Mysida (mysid)	0.001771	v94	0.0114778

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Table 5. Number of links for each sampled predator in the multiyear Gulf of Alaska food web network model.

Species or group node (top 50)	Links to predators	Links to prey	Total links per group
Gadus macrocephalus (Pacific cod)	3	166	169
Hippoglossus stenolepis (Pacific halibut)	3	115	118
Theragra chalcogramma (walleye pollock)	7	110	117
Atheresthes stomias (arrowtooth flounder)	6	72	78
Anoplopoma fimbria (sablefish)	2	58	60
Hippoglossoides elassodon (flathead sole)	4	44	48
Sebastolobus alascanus (shortspine thornyhead)	1	45	46
Sebastes alutus (Pacific ocean perch)	1	37	38
Microstomus pacificus (Dover sole)	2	15	17
Caridea (shrimp)	15		15
Pleurogrammus monopterygius (Atka mackerel)	3	12	15
Glyptocephalus zachirus (rex sole)	1	13	14
Osteichthyes: Teleostei (fish)	12		12
Euphausiacea (euphausiid)	12		12
Lepidopsetta sp. (rock sole type)	3	9	12
Unidentified organic material	11		11
Polychaeta (worm)	10		10
Gammaridea (amphipod)	10		10
Paguridae (hermit crab)	10		10
Crangonidae (shrimp)	9		9
Calanoida (copepod)	9		9
Non-gadoid fish remains	9		9
Pandalidae (shrimp)	9		9
Unidentified material	9		9
Themisto sp. (amphipod)	8		8
Hippolytidae (shrimp)	8		8
Pandalus borealis (shrimp)	8		8
Pandalus sp. (shrimp)	8		8
Cephalopoda (squid and octopus)	8		8
Zaprora silenus (prowfish)	1	7	8
Limanda aspera (yellowfin sole)	2	6	8
Bivalvia (clam)	7		7
Gastropoda (snail)	7		7
Chionoecetes sp. (snow and Tanner crab)	7		7
Teuthoidea (squid)	7		7
Pleuronectidae (flatfish)	7		7
Ampeliscidae (amphipod)	7		7
Crangon communis (shrimp)	7		7
Mysidae (mysid)	7		7
Isopoda (isopod)	7		7
Thysanoessa inermis (euphausiid)	7		7
Hemilepidotus jordani (yellow Irish lord)	1	6	7
Cottidae (sculpin)	7		7
Holmesiella anomala (mysid)	7		7
Neomysis czerniawskii (mysid)	7		7
Zoarcidae (eelpout)	7		7
Chionoecetes bairdi (Tanner crab)	6		6
Mallotus villosus (capelin)	6		6
Cyclopteridae (snailfish)	6		6
Octopoda (octopus)	6		6
All others	710	4	714
Total links	1037	719	1756

Note: Directed links are asymmetrical because of the food web assembly method using maximum links observed in a given year; the years included differ for some predator versus prey links at some nodes.

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Table 6. Number of links for each sampled predator in the 2001 Gulf of Alaska food web network model.

Species or group node (top 50)	Links to predators	Links to prey	Total links per group
Gadus macrocephalus (Pacific cod)	3	158	161
Hippoglossus stenolepis (Pacific halibut)	1	142	143
Atheresthes stomias (arrowtooth flounder)	4	87	91
Theragra chalcogramma (walleye pollock)	7	84	91
Anoplopoma fimbria (sablefish)		84	84
Glyptocephalus zachirus (rex sole)		61	61
Microstomus pacificus (Dover sole)		40	40
Sebastolobus alascanus (shortspine thornyhead)	3	35	38
Hippoglossoides elassodon (flathead sole)	2	26	28
Lepidopsetta bilineata (rock sole)	2	24	26
Lepidopsetta polyxystra (northern rock sole)		26	26
Dasycottus setiger (spinyhead sculpin)	3	21	24
Sebastes aleutianus (rougheye rockfish)		24	24
Sebastes alutus (Pacific ocean perch)	2	22	24
Gammaridea (amphipod)	20		20
Polychaeta (worm)	19		19
Sebastes borealis (shortraker rockfish)		19	19
Pleurogrammus monopterygius (Atka mackerel)		17	17
Amphipoda: Hyperiidea (amphipod)	16		16
Caridea (shrimp)	16		16
Hippolytidae (shrimp)	16		16
Thaleichthys pacificus (eulachon)	5	11	16
Euphausiidae (euphausiid)	15		15
Osteichthyes: Teleostei (fish)	15		15
Thysanoessa inermis (euphausiid)	15		15
Bivalvia (clam)	14		14
Albatrossia pectoralis (giant grenadier)		14	14
Euphausiacea (euphausiid)	14		14
Malacocottus zonurus (darkfin sculpin)	1	13	14
Pandalidae (shrimp)	14		14
Isopoda (isopod)	13		13
Mysidacea: Mysida (mysid)	13		13
Paguridae (hermit crab)	13		13
Cumacea (cumacean)	12		12
Thysanoessa sp. (euphausiid)	12		12
Chionoecetes bairdi (Tanner crab)	11		11
Pandalus sp. (shrimp)	11		11
Unidentified organic material	11		11
Crangonidae (shrimp)	10		10
Natantia (shrimp)	10		10
Pandalus borealis (shrimp)	10		10
Phyllodocidae (polychaete)	10		10
Reptantia (crab)	10		10
Calanoida (copepod)	9		9
Crangon sp. (shrimp)	9		9
Nephtyidae (polychaete)	9		9
Non-gadoid fish remains	9		9
Aphroditidae (sea mouse)	8		8
Bathymaster signatus (searcher)	1	7	8
Cephalopoda (squid and octopus)	8		8
All others	605	96	701
Total links	1011	1011	2022

Note: Directed links are symmetrical because the same data set was used to describe the links in each direction.

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thought experiment expands on the argument; theoretically, if increased sampling detected a few additional highly connected species that we had missed previously, the functional form of the degree distribution might remain the same, with a few highly connected species and many species with few links. To depart from the current scale-free degree distribution and move towards the Poisson or exponential distribution characteristic of a random network, all of the nodes added through additional sampling of groundfish predators and prey would need to have almost exactly the mean number of links per node expected for the whole network, and these new nodes would have to greatly outnumber the currently observed nodes with only one link (currently about one-third of nodes in each food web). The new nodes would also have to avoid attaching to the currently observed, highly connected groundfish nodes as well, because that would exaggerate the scale-free degree distribution. Of course, the addition of more diverse species might change the degree distribution to one resembling neither the power law nor the Poisson distribution, making the network more difficult to classify within the current descriptions.

Finally, even if the larger food web is not fully included in the network analysis, studying the groundfish-centered portion of the food web has some merit because this portion of the food web may represent a disproportionate amount of the energy flow in the GOA marine ecosystem. Within the context of the whole-ecosystem biomass distribution and predation rates reported in the only other food web of the western GOA (Aydin et al. 2007), groundfish account for the vast majority of predator biomass and consumption in the system. Therefore, the remainder of this discussion assumes that for practical purposes, the observed small-world diameter, the scale-free degree distribution, and the persistent set of highly connected nodes are true properties of the GOA food web.

General food web network properties?

Very few other studies have modeled food webs as simple undirected networks to explore whether they have random, small-world, and (or) scale-free network properties, perhaps because detailed food webs are difficult to construct or find in the scientific literature. In fact, five of the six existing studies exploring food web network properties used the same three (Solé and Montoya 2001; Montoya and Solé 2002) to seven (Camacho et al. 2002; Williams et al. 2002; Garlaschelli et al. 2003) food webs for all of their analyses, all of which were considered complete, but with one exception that had fewer than 100 species represented. The sixth study was more comprehensive, adding nine food webs to the previously studied seven, but even this study had only two food webs of comparable scale with the GOA in terms of number of species represented (Dunne et al. 2002). Therefore, even the incomplete GOA food webs built here appear to be more detailed than most previously studied food webs.

While there is general agreement that food webs are not random networks (Proulx et al. 2005 describe this as "the trivial hypothesis", p. 350), the existing studies disagree on whether food webs are more effectively modeled as small-world or scale-free networks. Despite the relatively small sample size, some have found clear evidence of universal scale-free degree distributions (Montoya and Solé 2002), while others found clear evidence of universal exponential degree distributions (Camacho et al. 2002); the most comprehensive study found both scale-free and exponential degree distributions depending upon the food web examined (Dunne et al. 2002). Similarly, some studies clearly identify food webs as small-world networks (Solé and Montoya 2001; Montoya and Solé 2002), while others suggest that food webs must be smaller small worlds — have less than three degrees of separation — relative to social or physical networks to display meaningful properties based on short path lengths (Williams et al. 2002). Still other studies imply that food webs are not small-world networks above a certain network size and generally never have the high clustering coefficients associated with social small-world networks, and therefore food webs are generally not small-world networks (Dunne et al. 2002). In some of these studies, the search for one universal, generalized model explaining all food webs has priority over the interpretation of the data from specific food webs. Furthermore, small-world and scale-free describe both specific network models and empirical properties observed in real networks. Rather than choosing between models to determine which is "right", it seems most practical to use the models to describe the empirical properties of the GOA food web network, especially if these modeling approaches are to be used in ecosystem-based fishery management applications.

The GOA food web networks exhibit a mix of the characteristics observed in all of the previous studies. For example, the degree distributions were best fit by a power law, as Montoya and Solé (2002) found for several lake and estuarine food webs. The GOA fits had equal (0.79) or higher (0.89) R^2 values relative to those estimated in Montoya and Solé (2002), and the estimated power law exponents of 0.9689 and 0.9782 for the GOA compare well with those found for aquatic food webs by Montoya and Solé (2002), which range from 0.94 to 1.13. This suggests that the GOA may have scale-free network properties, even if not all food webs do. The small-world property of short average path length is displayed in the GOA food webs, which have average path lengths around 2.6. As suggested by Williams et al. (2002), the small-world average path length only matters in a food web if it is less than 3. This is because the indirect effects with path length 2 (competition for common prey, support of a common predator, consumption of a predator, or support of a prey of a given species) can have similar impacts to a species as direct path length 1 (predator–prey) effects, but these impacts tend to damp out beyond three links. This suggests that the GOA may have the property that impacts on a single species may be felt rapidly through much of the food web because of its (small enough) small-world average path length, even if, like many other food webs (Dunne et al. 2002), it does not display the high average C values expected for a classic small-world network. While average C values were small and comparable with those from random networks, the GOA food web networks had very different distributions of C values from random networks, with a handful of the highest degree nodes having the highest C values (a result which seems intuitive). Overall, the GOA food web network

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results are consistent with those found in studies of other food webs, especially in identifying where food web networks share properties with social and physical networks and where they have different properties.

Attack, fragmentation, and preferential connection in food webs?

The scale-free network property most commonly cited is its robustness to error or the loss of nodes at random, combined with its vulnerability to attack or the loss of the highly connected nodes, which has been shown for both physical and social networks (Albert et al. 2000; Newman 2003) as well as for scale-free food webs (Solé and Montoya 2001). This property is easy to translate into a practical management context: if there is concern about maintaining food web structure, it is not necessary to worry about all chance species impacts due to fishing or environmental change because the scale-free food web is inherently robust to these events. However, knowing which are the highly connected nodes suggests that extra vigilance be given to protecting these species from attack (severe fishing effects or other environmental effects) to prevent single-species fishing impacts from translating into network fragmentation, especially if the hub species are already commercially fished species (as Pacific cod, Pacific halibut, and walleye pollock certainly are). However, two questions have less obvious answers.

First, what exactly does it mean to fragment a food web network? A connected food web network implies energy flow between links through the nodes. One possible outcome of fragmentation is that energy flow might be restricted to small subsets of the former network and might not reach all formerly connected nodes; in the extreme, Solé and Montoya (2001) assumed that these disconnected nodes would eventually go extinct for lack of sufficient energy flow. This is an oversimplification of a dynamic system such as a food web, where species (nodes) formerly linked by a pathway through one node (prey) would likely adapt to the loss of that pathway by switching to another prey if possible, thus establishing a new connection. In contrast with mass extinction being the likely outcome of fragmentation due to the loss of a highly connected node, reorganization of the food web seems more likely. This type of dramatic (and irreversible) change in ecosystem state has been observed in heavily fished marine ecosystems, for example, on Georges Bank in the North Atlantic (Fogarty and Murawski 1998). In that ecosystem, fishing mortality rates were more than triple the recommended rates for many exploited species for approximately 20 years, after which the rates were reduced (because the stocks collapsed). More than 10 years after management reduced fishing mortality to encourage rebuilding of the stocks, the recovery predicted from single stock models has not been observed (O'Brien et al. 2005). In contrast, the relative temporal stability suggested by the similar structures of the multiyear and 2001 food webs in the GOA coincided with a period of well-managed fisheries (Crockett 2005; Ruff 2005).

Rice (2001) outlines the important role of competition in food webs, which provides an explanation for why the loss of a highly connected species from the food web network might lead to an unpredictable and perhaps irreversible system reorganization. He draws a distinction between contest competition and scramble competition: contest competition involves behavioral or physiological adaptations that have evolved over time; in contrast, scramble competition is based on sudden, severe shortages or surpluses and has less to do with adaptation and more to do with which population has the best (luckiest) adjustment to the radical change in food supply rate (Valiela 1995). Rice suggests that contest competition is the basis for traditional ecological models of competitive exclusion, while scramble competition probably dominates real systems subject to environmental variability (or in this case, structural variability). The outcome of scramble competition is highly dependent on initial conditions (relative abundance of alternate prey and the predators) so that the community structure that resulted after a bout of scramble competition brought on by changes in abundance of a critical species might be highly unpredictable. Rice identified critical species as those occupying energy bottlenecks at the middle trophic levels; this may parallel the highly connected species in a scale-free network in that system energy flow is potentially altered significantly by effects to few single critical species. In this way, we can view network fragmentation as a threshold where the existing food web structure reorganizes into a new, perhaps unpredictable structure. In addition, this threshold may be related to the depletion of a stock occupying a highly connected node, as opposed to its complete extinction.

A second and perhaps more difficult question remains regarding the scale-free network concept, which is based on a model of growth wherein the system expands by adding nodes with preferential attachment of new nodes to existing high degree nodes; viz., is this a useful description of the process by which actual food webs develop over time? This has not been adequately explored in the existing literature. One possibility is that this process does not apply at all and that the observed degree distribution is just a sampling effect rather than a network property. However, this possibility was considered and dismissed above. Another possibility suggested by Camacho et al. (2002) is the existence of a few, abundant, preferred prey species with links to many predators in the system. While conceptually feasible, this was not the mechanism at work in the GOA food webs. Because we constructed the networks from the groundfish food habits database, most nodes in the GOA food web networks are the prey of groundfish, while fewer are predators as well as prey, and the highly connected nodes are the major groundfish predators with many prey links. Under these circumstances, the addition of a new prey node would occur if a predator consumed a new species. Presumably, prey prefer not to be consumed at all, so the "preferential attachment" argument is difficult to support from the prey node standpoint. However, from the predator node standpoint, predators with diverse diet preferences (e.g., cod) may be more likely to try new prey and by definition would already have many prey links. Therefore, the existence of certain predators with a highly diverse foraging strategy could help explain the scale-free degree distribution observed in the GOA food webs. While this mechanism is speculative at present, and other speculations may be equally valid, further behavioral studies of predator–prey interactions in marine ecosystems would provide more insight into the development of

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scale-free network structures, which have important management implications.

Management implications

Ecological networks are increasingly recognized as simultaneously resilient and fragile because of network structural properties (Montoya et al. 2006). Overall, simple network models have the ability to both capture the inherent complexity of ecosystems and identify system-level properties suggesting how impacts focused on a few species might spread to others through short interaction chains and to identify those species supporting critical structural connections. This is a potentially powerful result that fishery managers could use to promote ecosystem sustainability. First, it suggests that system-level thresholds exist and can be triggered by impacts to a tiny minority of nexus species in the system. However, this apparently bad news has especially good news associated with it; it is possible to identify that critical minority of species. Rather than worrying about each of thousands of species in the system individually, management can first focus on protecting the highly connected species in the network to avoid structural impacts of fishing on the food web, both through fragmentation and impact transfer via short average path lengths throughout the network. In the case of the GOA, these highly connected species are also the high biomass species that are commercially fished: Pacific cod, Pacific halibut, walleye pollock, and arrowtooth flounder. These species are highly dynamic, interdependent groups, responsible for considerable energy flow in the GOA (Aydin et al. 2007). They also exhibit a wide range of body sizes, especially Pacific cod and halibut, which potentially increases the strength of their predator–prey interactions and therefore the cascading effects of any perturbations to their populations (Woodward et al. 2005). While we did not address interaction strengths in this study, it is the next logical step to refine management advice. If it is true that the loss, severe depletion, or radical change in size structure of one or more of these species could disconnect a majority of predator–prey links in the system, then the potential for system reorganization after such a loss would be high. In this sense, appropriate fishery management for Pacific cod, Pacific halibut, walleye pollock, and arrowtooth flounder as single species would also prevent catastrophic system-level effects — but the relationships between these four species suggest that the current approach of single species management would be more appropriate placed within an ecosystem context. Network analysis provides a simple look at structural relationships between species and their potential impact on complex system behavior under perturbation. The essential property of the network proves to be its robustness to random disturbance combined with its vulnerability to very specific types of perturbation.

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Dynamics of bacteria–substrate stable isotope separation: dependence on substrate availability and implications for aquatic food web studies

Daryl J. McGoldrick, David R. Barton, Michael Power, Ryan W. Scott, and Barbara J. Butler

Abstract: Heterotrophic bacteria growing without substrate limitation discriminate against the heavier stable isotopes of C and N, which is reflected in the isotopic signatures of consumers of bacteria. We measured bacteria and substrate isotopic separation (C and N) during glucose and ammonium uptake by three strains of bacteria (*Pseudomonas putida*, *Bacillus megaterium*, and *Enterobacter aerogenes*) grown in batch culture at 4 and 30 °C. Isotopic separation between bacteria and substrate was dependent on substrate availability. Higher discrimination against the heavier isotopes, and therefore more depleted $\delta^{13}C$ and $\delta^{15}N$ values of bacterial biomass, were observed during the exponential growth phase when the nutrient supply was in excess of the demand. We also compared the isotopic ratios of *Chironomus tentans* grown on aged macrophyte detritus and commercial fish food. Isotopic signatures of *Chironomus* larvae grown on fish food were within the ranges typical of one trophic step, whereas larvae grown on detritus were strongly depleted in ^{13}C, suggesting assimilation of bacteria that had grown on the C-rich detritus. Our results are consistent with the very few other studies of bacterial fractionation of nonlimiting nutrients and may also explain the frequent observation of unexpectedly depleted isotopic signatures in aquatic food web studies.

Résumé : Les bactéries hétérotrophes qui croissent sans limitation de substrat sont capables de rejeter les isotopes stables plus lourds de carbone et d'azote, un phénomène qui se reflète dans les signatures isotopiques des consommateurs de bactéries. Nous avons mesuré la séparation des isotopes (de C et de N) dans les bactéries et le substrat durant l'absorption de glucose et d'ammonium par trois souches de bactéries (*Pseudomonas putida*, *Bacillus megaterium* et *Enterobacter aerogenes*) élevées en culture discontinue à 4 °C et à 30 °C. La séparation isotopique entre les bactéries et le substrat dépend de la disponibilité du substrat. On observe un plus fort rejet des isotopes plus lourds, et ainsi des valeurs réduites en $\delta^{13}C$ et en $\delta^{15}N$ de la biomasse bactérienne, durant la phase de croissance exponentielle lorsque l'apport de nutriments dépasse la demande. Nous avons aussi comparé les rapports isotopiques chez des *Chironomus tentans* Fabricius élevés sur du détritus de macrophytes vieilli et sur des aliments commerciaux pour poissons. Les signatures isotopiques des larves de *Chironomus* élevées sur des aliments pour poissons se situent dans la gamme des valeurs typiques d'un échelon trophique, alors que les larves élevées sur le détritus ont une forte carence en ^{13}C, ce indique une assimilation des bactéries qui se sont développées sur le détritus riche en carbone. Nos résultats sont en accord avec les très rares études sur la fractionation bactérienne des nutriments non limitants et ils peuvent aussi expliquer l'observation fréquente de signatures isotopiques à carence inattendue dans les études des réseaux alimentaires aquatiques.

[Traduit par la Rédaction]

Introduction

The fundamental assumptions underlying the use of stable isotopes to elucidate elemental cycling and the structure of food webs are that the C isotopic signatures of consumers are similar to those of their prey (e.g., $\delta^{13}C = \pm 1‰$; DeNiro and Epstein 1978, 1981) and that N isotopic signatures vary predictably with each trophic transfer (e.g., $\delta^{15}N = +3.4‰$; Post 2002). If potential foods are isotopically distinct, it is relatively straightforward to define feeding relationships for organisms with signatures within these ranges.

It is not unusual, however, to find $\delta^{13}C$ values in aquatic consumers that do not seem to reflect the most abundant potential foods. For example, freshwater zooplankton (e.g., del Giorgio and France 1996; Grey and Jones 1999; Bastviken et al. 2003) and benthic macroinvertebrates (e.g., Mitchell et al. 1996; Finlay 2001; Grey et al. 2004) have often been reported to be ^{13}C-depleted relative to autochthonous or allochthonous sources of organic matter. This is especially common for profundal Chironomidae in lakes (e.g., Grey et al. 2004; Hershey et al. 2006).

Unexpectedly depleted ^{13}C values have been interpreted

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in several ways. For example, algae, rather than vascular macrophytes, could be the most important contributors to benthic secondary production in salt marshes and freshwater wetlands (e.g., Hullar et al. 1996; Schlacher and Wooldridge 1996; Boschker et al. 1999). Alternatively, the ^{13}C-depleted signatures of salt marsh detritivores may reflect assimilation of chemolithotrophic CO_2-utilizing sulfur bacteria that oxidize reduced sulfur compounds released by anaerobic sulfur-reducing bacteria in decomposing detrital organic matter (Peterson et al. 1980; Kharlamenko et al. 2001). Bunn and Boon (1993) suggested that ^{13}C depletion in the benthos of freshwater billabongs could indicate consumption by benthic organisms of ^{13}C-depleted methanotrophs that utilized biogenic methane produced within the anoxic sediments. Subsequent studies have suggested that methanotrophic bacteria can be important components of the diets of invertebrates in lakes and streams (e.g., Kiyashko et al. 2001; Bastviken et al. 2003; Kohzu et al. 2004).

Methanotrophic bacteria discriminate very strongly against ^{13}C when C is not limiting (Summons et al. 1994), and the same may apply to other organisms. For example, lotic periphyton is ^{13}C-depleted when growth rates are limited by light or temperature rather than by C or N (MacLeod and Barton 1998). The microbial communities growing on deciduous leaves in streams or dissolved organic C in lakes tend to be limited by nutrients such as N and P (e.g., Gulis and Suberkropp 2003; Smith and Prairie 2004) but not C.

These observations led us to hypothesize that aerobic heterotrophs might also discriminate against ^{13}C when C is available in excess (e.g., when growing directly on coarse detrital particles; Baldy et al. 2002) and this would then be reflected in the isotopic signature of consumers of that bacterial biomass. To test this idea, we conducted a series of experiments. First, we cultured three common heterotrophic soil bacteria (two Gram-positive and one Gram-negative) on minimal media containing ammonia and glucose as the sole N and C sources and determined the $\delta^{13}C$ of the cells and the media throughout the batch culture cycle. If the cells discriminate in favour of lighter isotopes, they will be depleted in ^{13}C compared with the glucose during early growth when C is available. After the culture reaches stationary phase, ^{13}C depletion in the cells is not expected, as C will be recycled. Second, we compared the isotopic signatures of *Chironomus tentans* larvae fed commercial fish food with those of larvae fed aged detritus derived from aquatic macrophytes. We hypothesized that larvae fed on detritus would be depleted in ^{13}C relative to the bulk detrital signature if they were assimilating the microbial flora growing on essentially unlimited C. In natural systems, a similar situation may arise in lakes and streams where substantial inputs of particulate organic matter allow sustained bacterial activity.

Material and methods

Batch culture experiments

Inocula from frozen stock strains of *Pseudomonas putida* GR12-2, *Bacillus megaterium* ATCC 9885, and *Enterobacter aerogenes* ATCC 13048 from the University of Waterloo culture collection were incubated overnight in sterile tryptic soy broth with vigorous mixing at the optimal growth temperature for the culture (approximately 30 °C for all three strains). Seven hundred microlitre volumes of these cultures of *P. putida* and *B. megaterium* were inoculated into culture flasks containing 50 mL of 20% minimal salts medium (4 g·L^{-1} KH_2PO_4, 6 g·L^{-1} Na_2HPO_4, 0.2 g·L^{-1} $MgSO_4 \cdot 7H_2O$, 0.1 g·L^{-1} $FeSO_4 \cdot 7H_2O$, 2 g·L^{-1} glucose, and 2 g·L^{-1} $(NH_4)_2SO_4$), which were then incubated in a shaker at 30 °C. *Pseudomonas putida* was also incubated at 4 °C. The size of the initial inoculum used for *E. aerogenes* was the same (700 µL), but we used a different medium that contained relatively more N: 33.9 g·L^{-1} Na_2HPO_4, 15 g·L^{-1} KH_2PO_4, 2.5 g·L^{-1} NaCl, 5 g·L^{-1} NH_4Cl, 2.0 g·L^{-1} glucose, and 2 mL of 1 mol·L^{-1} $MgSO_4$) because of poor growth during the initial run (see below).

Initial culturing experiments were conducted to estimate rates of growth of each strain. The change in absorbance at 600 nm until stationary growth was monitored to create sampling schedules that sufficiently covered the exponential and stationary growth phases. For *B. megaterium* and *E. aerogenes*, samples were taken at half-hour intervals for 2.5 h beginning at 2.0 and 1.5 h, respectively, after the cultures were inoculated. Stationary-phase samples were taken 6–7 h after inoculation. For *P. putida*, samples were taken every hour for the cultures grown at 30 °C. Samples were taken every 24 h after the first 48 h from the 4 °C *P. putida* cultures to observe fractionation effects when growth was limited by temperature.

At each sampling interval, three replicate flasks of *B. megaterium* or *E. aerogenes* were removed from the incubator and 30 mL of culture was removed and centrifuged at approximately 7000 rpm for 12 min. The complete contents of a single flask of *P. putida* were centrifuged at each sampling interval. The cell-free medium was frozen; the cells were washed twice with sodium phosphate buffer (0.05 mol·L^{-1}, pH 7.0) and then frozen. Culture growth was monitored at each interval by measuring the absorbance of the culture at 600 nm with a spectrophotometer.

Glucose concentration in each sample of medium was assayed using the glucose–peroxidase method (GAGO-20; Sigma Diagnostics). The harvested cells and remaining cell-free media were dried at approximately 60 °C for isotope analysis.

Consumer experiment

A dipnet was used to collect living and dead submerged aquatic macrophytes and surficial sediment (sand) from the marsh at Long Point on Lake Erie, Ontario, Canada, in June 2001. The most abundant macrophyte in the area was *Chara* sp. ($\delta^{13}C$ = –16.9 3‰, $\delta^{15}N$ = 5.93‰) followed by *Vallisneria* sp. ($\delta^{13}C$ = –15.73‰, $\delta^{15}N$ = –0.523‰), *Potamogeton pectinata* ($\delta^{13}C$ = –14.43‰, $\delta^{15}N$ = 2.823‰), and *Myriophyllum spicatum* ($\delta^{13}C$ = –13.93‰, $\delta^{15}N$ = 7.083‰) (McGoldrick 2003). The material collected in the dipnet was washed in a 200 µm aperture net to remove fine sediments and stored at –20 °C until the experiment was started in April 2002.

The mixture of plant material and sand was placed in an aquarium, covered with well water, and then left at room temperature (approximately 20 °C) in darkness. After 4 weeks, the material was stirred thoroughly by hand and 150 mL of the aged detritus–sand and 350 mL of well water

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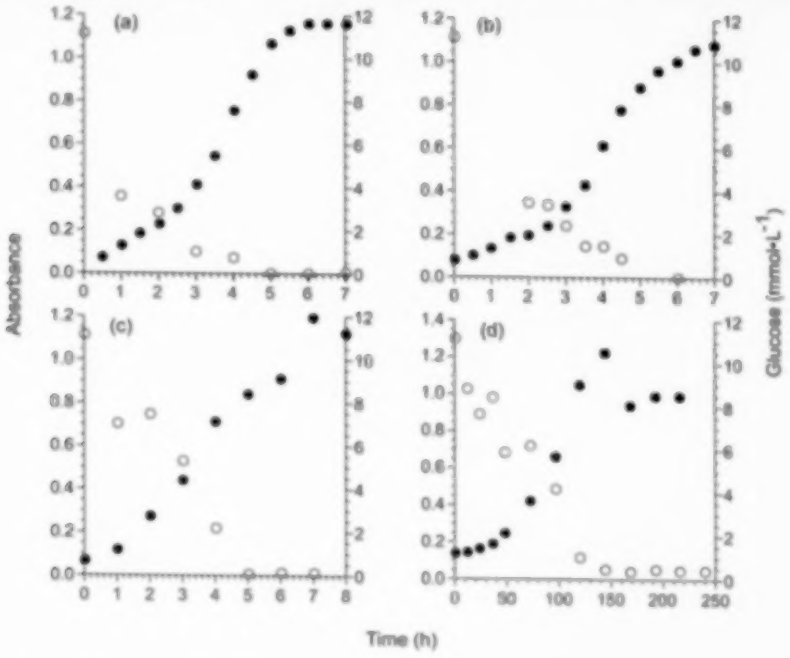
Fig. 1. Optical absorbance and glucose concentrations in cultures of (*a*) *Enterobacter aerogenes*, (*b*) *Bacillus megaterium*, and (*c*) *Pseudomonas putida* at 30 °C and (*d*) *P. putida* at 4 °C.



were added to each of six tall 1000 mL beakers. Six identical beakers received 150 mL of fine sterile sand containing no organic matter and 350 mL of well water. Individual egg masses from a laboratory culture of *C. tentans* were divided equally between a detritus-filled beaker and a sand-filled beaker, and three such pairs of beakers were placed in water baths at temperatures of 20 ± 1 and 30 ± 1 °C. Each water bath was covered with black plastic to exclude all light. *Chironomus* larvae in the sand-filled beakers were fed approximately 0.1 g of dry flaked commercial fish food (Tetramin, C:N = 6.833) every 3 days; no food was added to the detritus-filled beakers. Each beaker was aerated using an aquarium pump and airstones to prevent anoxia. After 30 days, a maximum of 20 third- or fourth-instar larvae were collected from each beaker. After removal of the digestive tracts, the larvae were dried at 60 °C, ground to a fine powder in a ball mill, and analysed for stable isotopes of C and N. Samples of Tetramin and the detritus from each beaker were collected during and after the experiment and these samples were dried, ground, and analysed for stable isotopes of C and N. Detrital C–N ratios averaged 20.3:1 at the beginning of the experiment and 23.9:1 at the end.

All samples for stable isotope analyses contained 1–3 mg of organic material (dry weight) and were analysed at the Environmental Isotope Laboratory, University of Waterloo, using a Micromass VG Isochrom (*P. putida* and *Chiromomus* experiments) or a Delta Plus (*B. megaterium* and *E. aerogenes*) continuous-flow stable isotope ratio mass spectrometer connected to a Carlo Erba elemental analyser with an analytic precision of ±0.2‰ for C and ±0.3‰ for N. Stable isotope ratios are expressed as delta values (δ) and are measures of the parts per thousand (‰ or per mil) difference between the isotope ratio of a sample and that of the appropriate international standard. The international standards used were carbonate rock from the Peedee Belemnite formation (Craig 1957) and nitrogen gas in the atmosphere (Mariotti 1983). By convention, all international standards are set at a value of 0‰.

Statistical methods

To account for simple dilution of the original isotopic composition of the bacterial cultures, we calculated the expected $^{13}C/^{12}C$ and $^{15}N/^{14}N$ signatures after each doubling, assuming no fractionation of C and N in the media. The regressions of these expected values against time were used to predict the expected isotopic signatures at the times when cells were harvested. A difference between observed and expected values indicates isotopic fractionation by the bacteria at each harvest.

Differences in the mean isotopic signatures of the detritus at the beginning and end of the consumer experiment were tested for significance using two-sample *t* tests (Brown and Rothers 1993). The form of the test statistic applied was determined after testing homogeneity of variance using *F* tests (Brown and Rothers 1993). Model I two-factor ANOVA was used to analyse consumer isotopic signatures (Zar 1999). Maximal type I error in all statistical tests was set at $\alpha = 0.05$.

Results

The three bacteria grew at similar rates at 30 °C, with doubling times of 1.06 h (*B. megaterium*), 1.19 h (*E. aerogenes*), and 1.20 (*P. putida*). All were in early stationary

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Fig. 2. Observed stable C isotope signatures relative to predicted values (mean ± 1 SE), assuming no isotopic fractionation, of *Pseudomonas putida* (open circles), *Bacillus megaterium* (open triangles), and *Enterobacter aerogenes* (solid triangles) grown at 30 °C and *P. putida* grown at 4 °C (solid circles). Values for *P. putida* represent single samples at each harvest.

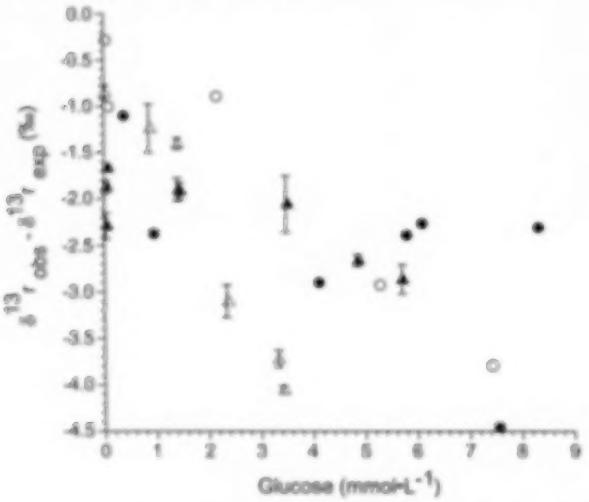
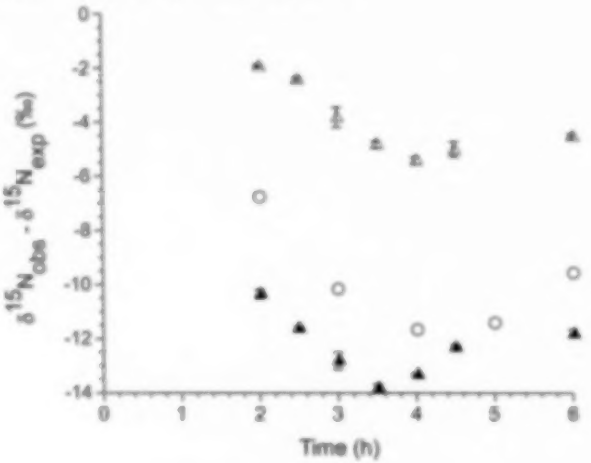


Fig. 3. Observed stable N isotope signatures relative to predicted values (mean ± 1 SE), assuming no isotopic fractionation, of *Pseudomonas putida* (open circles), *Bacillus megaterium* (open triangles), and *Enterobacter aerogenes* (solid triangles) grown at 30 °C and *P. putida* grown at 4 °C (solid circles). Values for *P. putida* represent single samples at each harvest.



phase by 6 h after inoculation (Fig. 1). The amount of glucose in the media mirrored bacterial growth (Fig. 1), reaching concentrations <0.02 mmol·L^{-1} after about five doublings (4.5–5.5 h). The growth of *P. putida* was much slower at 4 °C, with a doubling time of 39 h, and reached stationary phase by about 144 h. The glucose concentration in the medium approached zero by 120 h.

All culture media were made from the same stock of glucose with a $\delta^{13}C$ of –10.10‰. We used three different sources of ammonium sulfate so the $\delta^{15}N$ differed somewhat: –0.60‰ for *P. putida*, –3.07‰ for *B. megaterium*, and 1.52‰ for *E. aerogenes*. $\delta^{15}N$ of the inocula were 4.31‰ for *P. putida*, 0.26‰ for *B. megaterium*, and 0.11‰ for *E. aerogenes*; all of these had $\delta^{13}C$ values between –21.22‰ and –22.66‰.

All $\delta^{13}C$ signatures of harvested bacterial cells were depleted relative to predicted values (Fig. 2). The magnitude of this depletion decreased significantly (regression F statistic = 15.47, $p < 0.05$) with decreasing concentration of glucose in the culture medium. The average depletion was 2.74‰ when the glucose concentration of the medium was >1 mmol·L^{-1}.

Bacteria also discriminated against ^{15}N. Cells grown at 30 °C became increasingly ^{15}N-depleted during the first 3.5 to 4 h of incubation and then $\delta^{15}N$ stabilized or became slightly enriched during early stationary phase (Fig. 3). A similar pattern was observed for *P. putida* grown at 4 °C.

The abundances and sizes of *C. tentans* larvae suggested that survival was similar in both food treatments but larvae grew faster when fed the commercial food flakes. Not surprisingly, the rate of development was faster at 30 °C than at 20 °C: a few individuals had pupated by day 30 at the higher temperature. We did not attempt to measure oxygen concentrations in the sediment but saw no evidence of the characteristic blackening that would indicate anoxic conditions.

On average, larvae of *C. tentans* grown on macrophyte detritus from Little Rice Bay at 20 °C were depleted by 4.69 ± 1.05‰ in $\delta^{13}C$ and enriched in $\delta^{15}N$ by 5.00 ± 0.74‰ relative to the detritus (Table 1). Larvae grown at the same temperature and fed commercial food flakes were enriched in $\delta^{13}C$ by 1.81 ± 0.16‰ and in $\delta^{15}N$ by 4.85 ± 1.19‰ relative to their food source. Larvae grown on detritus at 30 °C were again depleted in $\delta^{13}C$ by 4.16 ± 1.24‰ and enriched in $\delta^{15}N$ by 5.34 ± 0.78‰ relative to the detritus. Larvae fed flakes at 30 °C were enriched in $\delta^{13}C$ by 1.41 ± 0.29‰ and in $\delta^{15}N$ by 4.50 ± 1.01‰ relative to their food source. The variability among replicates in the detritus treatments reflects the course nature of the material: the detritus was not homogenized prior to the beginning of the experiment. Two-factor ANOVA (Table 2) indicated a significant effect of treatment (detritus or flakes) on the mean change in $\delta^{13}C$ ($F_{[8,1]} = 71.03$, $p < 0.001$) but no effect of temperature ($F_{[8,1]} = 0.01$, $p = 0.930$) or interaction ($F_{[8,1]} = 0.43$, $p = 0.529$). For $\delta^{15}N$, there were no significant treatment ($F_{[8,1]} = 1.18$, $p = 0.310$), temperature ($F_{[8,1]} = 0.00$, $p = 0.997$), or interaction ($F_{[8,1]} = 0.56$, $p < 0.476$) effects. With the exception of the $\delta^{15}N$ values of the detritus in the 30 °C treatment, the isotopic signatures of the detritus at the start and end of the 30 day experiment showed no significant change in isotopic signatures (t test, 2 df, $p > 0.05$). In the 30 °C treatment, the $\delta^{15}N$ was 1.4‰ lower after the 30 day duration of the experiment.

Discussion

The results of our laboratory experiments confirmed our expectation that aerobic heterotrophic bacteria discriminate against the heavier isotopes of C or N when the supply of either element is not limiting. Bacterial cells grown in batch

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Table 1. Stable isotope signatures of aged aquatic macrophyte detritus, commercial fish food flakes, and larvae of *Chironomus tentans* grown for 30 days on each at 20 and 30 °C.

		$\delta^{13}C$			$\delta^{15}N$		
Food source	Temperature (°C)	Source	Larvae	Δ	Source	Larvae	Δ
Detritus	20	–13.04	–19.05	–6.01	4.20	8.88	4.67
Detritus	20	–14.07	–19.46	–5.39	3.57	8.90	5.33
Detritus	20	–15.81	–18.49	–2.68	3.46	8.45	4.99
Treatment mean ± SD				–4.69±1.05			5.00±0.74
Flakes	20	–22.71	–20.72	1.99	7.91	11.88	3.96
Flakes	20	–22.58	–20.99	1.59	8.08	13.96	5.88
Flakes	20	–22.73	–20.88	1.86	8.01	12.71	4.69
Treatment mean ± SD				1.81±0.16			4.85±1.19
Detritus	30	–12.90	–19.02	–6.12	3.58	7.94	4.36
Detritus	30	–15.79	–18.82	–3.03	3.06	8.80	5.74
Detritus	30	–13.45	–16.77	–3.32	2.66	8.59	5.92
Treatment mean ± SD				–4.16±1.24			5.34±0.78
Flakes	30	–22.71	–21.03	1.68	7.91	11.67	3.76
Flakes	30	–22.58	–21.23	1.35	8.08	12.40	4.32
Flakes	30	–22.73	–21.54	1.19	8.01	13.45	5.43
Treatment mean ± SD				1.41±0.29			4.50±1.01

Note: Δ defines the individual isotopic differences between harvested larvae and food source..

Table 2. ANOVA results for the consumer experiments using treatment (detritus and flakes) and temperature (20 and 30 °C) as the factors.

Source of variation	SS	df	MSS
$\delta^{13}C$			
Total	122.25	11	
Cells	109.94	3	
Treatment	109.26	1	109.26
Temperature	0.01	1	0.01
Treatment × temperature	0.67	1	0.67
Within cells	12.30	8	1.54
$\delta^{15}N$			
Total	6.08	11	
Cells	1.09	3	
Treatment	0.74	1	0.74
Temperature	0.00	1	0.00
Treatment × temperature	0.35	1	0.35
Within cells	5.00	8	0.62

Note: SS, df, and MSS define the sum of squares, degrees of freedom, and mean sum of squares, respectively.

cultures were depleted in ^{13}C relative to the initial C source as long as glucose was available in the medium. Cells harvested during stationary phase generally had $\delta^{13}C$ signatures that were more similar to that of the original C source. In the second experiment, large amounts of detritus derived from aquatic macrophytes still remained when *Chironomus* larvae were removed from the experimental beakers, so that any bacteria growing on the detritus likely still experienced an abundant C supply. The larvae were significantly ^{13}C-depleted relative to the detritus, suggesting that they had not assimilated macrophyte C directly but rather via microbial flora actively growing on the plant material. The alternative explanation, that larvae fed selectively on pieces of *Elodea canadense* ($\delta^{13}C$ = –18.06; McGoldrick 2003), is very improbable given the signatures of the detritus, the fairly consistent differences between larval and detrital signatures, and the low abundance of *E. canadense* in the marsh (<6% of total cover).

Bacteria also discriminated against ^{15}N in the N-rich culture media. Both Tetramin and macrophyte detritus contained proportionally less N, and the enrichment in ^{15}N signatures of *Chironomus* were within the range of values that have been reported for one trophic step (e.g., Adams and Sterner 2000; Post 2002). Microbial growth on dead plant tissue in aquatic habitats is often limited by the availability of nutrients such as N and P (e.g., Meyer and Johnson 1983; Gulis and Suberkropp 2003).

Isotopic separation resulting from fractionation can be influenced by the substrate on which bacteria are grown (Macko and Estep 1984; Hunkeler et al. 1999; Hunkeler and Aravena 2000), but it is generally assumed that the isotopic signatures of bacteria from natural environments should be similar to those of their sources of C (Boschker et al. 1999). In some studies, although not all, bacterial biomarkers reflect the isotopic composition of the substrate, but different fractionation effects during the synthesis of specific compounds complicate the interpretation of such observations (Boschker and Middleburg 2002). Laboratory studies have shown little or no isotopic fractionation by aerobic bacteria growing on labile substrates such as glucose or macrophyte leachate (e.g., Blair et al. 1985; Coffin et al. 1990; Hullar et al. 1996). In those studies where whole cells were subjected to stable isotope analysis, however, cultures were harvested relatively late in the growth cycle. Our data suggest that nutrients are being recycled within the culture by this point, causing a reduction in isotopic separation.

Summons et al. (1994) found that methanotrophic bacteria discriminated more strongly against ^{13}C early in exponential growth phase than they did later as substrate concentrations declined. However, fractionation was constant in the presence of excess substrate. Similarly, the CO_2 evolved during growth on complex or somewhat refractory substrates may be ^{13}C-depleted (Mary et al. 1992; Barth et al. 2000), and

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isotopic enrichment of the substrate during the course of microbial utilization is commonly observed (e.g., Blair et al. 1985; Barth et al. 2000; Goedkoop et al. 2006). Fractionation of stable isotopes of N by the marine bacterium *Vibrio harveyi* varied with the concentration of ammonium in the culture medium, ranging from –27 ‰ to –14‰ (Hoch et al. 1992). The strong isotopic separation between bacterial cells and NH_4^+ indicates that N was never limiting in our cultures.

We suggest that assimilation of ^{13}C-depleted bacteria that have grown on particles of detritus is the simplest explanation for many reports of what appear to be anomalously depleted signatures in a variety of animals. Freshwater zooplankton are often ^{13}C-depleted relative to particulate organic matter, and this has been attributed to selective consumption of only the smallest size fractions (e.g., Mitchell et al. 1996; Grey and Jones 1999), which may have depleted signatures because of photosynthetic incorporation of isotopically light (i.e., ^{13}C-depleted), biogenic CO_2 (del Giorgio and France 1996; France et al. 1997). ^{13}C depletion in benthic macroinvertebrates, especially Chironomidae and Bivalvia, relative to potential autochthonous or allochthonous sources of organic matter in lakes is often attributed to consumption of methanotrophic bacteria (e.g., Grey et al. 2004; Sierszen et al. 2004; Hershey et al. 2006). Similarly, unexpectedly low ^{13}C values have been interpreted to mean that algae, rather than vascular macrophytes, are the most important contributors to benthic secondary production in salt marshes (e.g., Fry 1984; Schlacher and Wooldridge 1996; Boschker et al. 1999). In each of these situations, bacteria would most likely be associated with C-rich detrital particles (e.g., Bouk and Goulder 1983; Van Mooy et al. 2001; Baldy et al. 2002). Consumption of actively growing bacteria, and perhaps the exopolymers that make up the bulk of the matrix in which they actually live (Hall and Meyer 1998), would yield depleted $\delta^{13}C$ values, even in animals that obtain only part of their C from bacterial sources (Nichols and Garling 2000).

It has long been known that bacteria and fungi are important in the breakdown of allochthonous organic matter in streams, increasing the palatability of autumn-shed leaves to shredding invertebrates (Kaushik and Hynes 1971; Suberkropp and Klug 1976; Gulis and Suberkropp 2003). Assimilation of the bacteria associated with detrital particles has been shown to be important to a variety of consumers (Adams and Agelovic 1970; Baker and Bradnam 1976; Hall and Meyer 1998). With few exceptions (e.g., Nichols and Garling 2000), investigators using stable isotopes to elucidate trophic relationships have not recognized direct consumption of bacteria other than methanotrophs or sulfur-oxidizing chemoautotrophs (Bunn and Boon 1993; Kharlamenko et al. 2001; Kiyashko et al. 2001). Our observations suggest that the hypothesized sequences of C flow to explain the depleted $\delta^{13}C$ of invertebrates in coastal wetlands (e.g., macrophytes → decomposer bacteria → DIC → planktonic algae → consumers; Keough et al. 1996) or backwaters of a stream (allochthonous litter → methanogenic bacteria → methanotrophic bacteria → consumers; Kohzu et al. 2004) may contain more links than are necessary.

Large quantities of organic detritus are common in many aquatic habitats, particularly wetlands, deeper basins of lakes, and depositional zones in streams. The bacterial communities living on detrital particles can be expected to be $\delta^{13}C$-depleted because they will rarely be C-limited. Recognition of these microbial processes is essential to the appropriate interpretation of aquatic food webs from stable isotope analyses.

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Quantifying age-reading error for use in fisheries stock assessments, with application to species in Australia's southern and eastern scalefish and shark fishery

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Abstract: Age-reading error occurs when estimates of age based on reading hard structures differ from the true age of the animal concerned. This error needs to be accounted for when conducting stock assessments. Common methods for quantifying age-reading error include the average percent error, the coefficient of variation, age bias plots, and age difference tables, but these techniques cannot be used to construct age-reading error matrices. A method for constructing age-reading error matrices that accounts for both ageing bias and ageing imprecision is outlined. Simulation evaluation of this method suggests that it is able to estimate both ageing bias (assuming that one reader is unbiased) and ageing imprecision for relatively large sample sizes and for the ages that constitute the bulk of the ages in the sample. However, the performance of the method is poor when sample sizes are small, age-reading error is correlated among readers, when both readers are biased, and for ages that are poorly represented in the sample. The method is applied for illustrative purposes to data on multiple-aged fish in Australia's southern and eastern scalefish and shark fishery.

Résumé : Les erreurs de lecture de l'âge se produisent lorsque les estimations de l'âge basées sur la lecture de structures dures diffèrent de l'âge réel de l'animal en question. Il est nécessaire de tenir compte de cette erreur dans les évaluations de stocks. Les méthodes courantes pour quantifier l'erreur de lecture de l'âge comprennent le pourcentage moyen d'erreur, le coefficient de variation, les graphiques d'erreur en fonction de l'âge et les tables de différences d'âge, mais ces méthodes ne peuvent pas servir à contruire des matrices d'erreurs de lecture de l'âge. Nous décrivons une méthode pour contruire des matrices d'erreurs de lecture de l'âge qui tiennent compte autant de l'erreur que de l'imprécision de la détermination de l'âge. Une évaluation de la méthode par simulation indique qu'elle est capable d'estimer tant l'erreur de la lecture d'âge (si on suppose qu'un des lecteurs n'est pas biaisé) que l'imprécision de la détermination d'âge pour des échantillons de taille relativement élevée et pour les âges qui constituent la majorité des âges dans l'échantillon. Cependant, la performance de la méthode est médiocre lorsque l'échantillon est petit, lorsqu'il y a corrélation de l'erreur de lecture entre les lecteurs, lorsque les deux lecteurs sont biaisés et pour les âges qui sont peu représentés dans l'échantillon. Comme exemple, nous appliquons la méthode à des données de poissons d'âges multiples obtenues des pêches commerciales de poissons à écailles et de requins du sud et de l'est de l'Australie.

[Traduit par la Rédaction]

Introduction

Quantitative stock assessments that involve fitting population dynamics models to data collected from fishery-dependent and -independent sampling programs are an important component of the basis for the scientific management advice for many of the world's major fisheries. Many of the stock assessments conducted for marine species off New Zealand, Australia, South Africa, and the west coast of North America are currently based on the integrated analysis paradigm (e.g., Fournier and Archibald 1982; Methot 2000, 2007). Integrated analysis assessments can make use of a wide range of data types, including indices of relative and absolute abundance, catch and survey age and size composition information, and tagging data. Central to the use of age composition data in stock assessments based on integrated analysis is the relationship between the ages obtained by reading hard structures such as otoliths and spines and the

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true age of the animal. There are two sources of uncertainty in this relationship, bias and imprecision, both of which occur regularly. Ageing bias occurs when there is a systematic difference between the true age of an animal and the age assigned to it, whereas ageing imprecision occurs when age-reading errors occur at random. Reeves (2003) examined the impact of age-reading error on the performance of stock assessments based on extended survivors analysis (Shepherd 1999), an assessment framework that ignores age-reading error. Reeves (2003) found that although estimates of spawning stock biomass and fishing mortality were broadly correct, those of recruitment were smoothed out and those of total allowable catch under a control rule that approximates how International Council for the Exploration of the Sea advice is provided were too optimistic in the presence of age-reading error. The smoothing of recruitment estimates leads to difficulties when estimating a stock–recruitment relationship, quantifying the risk associated with future management strategies, and determining the impact of environmental factors on recruitment (Fournier and Archibald 1982; Richards et al. 1992).

In principle, age-reading error can be represented using a matrix that specifies the probability of an animal of true age a being aged to be that age or some other age a', $P(a'|a)$. The model predictions upon which the likelihood component in the stock assessment for the age composition data is based are then a function of the model estimate for the observed catch of animals of age a after accounting for age-reading error. Given $P(a'|a)$, this prediction would be

$$(1) \qquad C_{a'} = \sum_{a} P(a'|a)C_a$$

where C_a is the model estimate of the catch of animals of age a, and $C_{a'}$ is the model estimate of the catch of animals of (perceived) age a' after accounting for age-reading error.

The ability to take account of age-reading error is already included in several of the most commonly applied stock assessment packages, e.g., stock synthesis (Methot 2000, 2007), Coleraine (Hilborn et al. 2003), and CASAL (Bull et al. 2003), but these packages do not include the facility to estimate age-reading error matrices.

The extent of age-reading imprecision and bias is regularly assessed using measures such as the average percent error (APE) (Beamish and Fournier 1981), the coefficient of variation, age bias plots (Campana et al. 1995), and age difference tables (Morison et al. 1998), but these measures cannot be used to construct age-reading error matrices for use in stock assessments because they focus on either precision or bias but not both. Richards et al. (1992) developed a method for estimating the parameters of functions that could be used to model the relationship between true and estimated age and hence construct the function $P(a'|a)$. This method, which has unfortunately not been used much in practice, perhaps because of its relative complexity, is based on maximum likelihood and allows for considerable flexibility in the relationship between (true) age and the expectation and imprecision of the estimate of this age.

This paper first conducts a simulation study to determine the performance of an extension of the method developed by Richards et al. (1992) given different sample sizes (numbers of animals read by two or more readers) and the structure of the relationship between true and estimated age for the particular case of silver warehou (*Seriolella punctata*) (previously also known as spotted warehou). The ability of model selection methods based on the Bayesian information criterion (BIC) (Schwarz 1978) to correctly detect the nature of age-reading error is also assessed for this species. It then applies the method to estimate age-reading error for another seven species in Australia's southern and eastern scalefish and shark fishery.

Materials and methods

Data and ageing protocol

The data used in the analyses of this paper were obtained from the Central Ageing Facility (CAF) (Queenscliff, Victoria, Australia), a specialist fish-ageing laboratory established in Australia during the early 1990s (Morison et al. 1998). The CAF is a fully integrated processing and ageing unit that has provided age estimates for more than 200 species ranging from temperate to tropical species and from freshwater species to species found on the continental slope and on seamounts.

Otoliths are collected from the southern and eastern scalefish and shark fishery throughout the year, and the entire year's sample is read after all of the otoliths have been collected. This provides for efficiency and requires fewer calibration checks of readers. It helps maintain consistency by reducing the likelihood of a change or drift over time in interpretation of the incremental structure. APE, age bias plots, and age difference tables are used qualitatively to determine bias and precision. Specifically, if a new reader is assigned to a species or a substantial amount of time has elapsed since a particular species has been last aged (maximum >1 month), the reader reads a subset of 100 otoliths from a calibration set (previously aged otoliths from various years) and APE and age bias plots are examined. If the APE is <5% and there is no evidence for bias, then the reader is allowed to continue. As such, an APE >5% is considered to indicate poor precision, an extremely difficult species to age, or insufficient training of new readers. A more detailed description of the ageing procedures used by the CAF can be found in Morison et al. (1998).

Data from eight species are used in this paper: silver warehou, blue grenadier (*Macruronus novaezelandiae*), school whiting (*Sillago flindersi*), tiger flathead (*Platycephalus richardsoni*), deepwater flathead (*Platycephalus conatus*), pink ling (*Genypterus blacodes*), gemfish (*Rexea solandri*), and black bream (*Acanthopagrus butcheri*). The analyses for school whiting and gemfish are based on whole otolith readings, while those for the remaining species (except silver warehou) are based on reading of sectioned otoliths. The analyses for silver warehou also include readings based on whole otoliths to illustrate how ageing bias can be quantified.

The total number of samples aged at the CAF for each species examined in this study and the numbers of repeat reads (secondary and tertiary) by reader available for inter- and intra-rereader comparisons are provided in Table 1. The reader index (A, B, C, etc.) in Table 1 refers to specific readers, not necessarily the primary, secondary, or tertiary age estimate. The primary reads of otoliths for a new species

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Table 1. Numbers of samples aged at the Central Ageing Facility for each species examined in this study and the numbers of repeat reads (secondary and tertiary) by reader.

			Maximum age (years)	Reader A			Reader B			Reader C			Other readers			
Scientific name	Family	Habitat		1st	2nd	3rd	1st	2nd	3rd	1st	2nd	3rd	1st	2nd	3rd	Whole
Seriolella punctata	Centrolophidae	Marine, temperate	23		36		2703	1407	31							1480
Macruronus novaezelandiae	Merlucciidae	Marine, temperate	25	940						4520	4512					940
Sillago flindersi[a]	Sillaginidae	Marine, temperate	8	160				184					758	719	122	
Platycephalus richardsoni	Platycephalidae	Marine, temperate	25		101		541	276		420	332	72	314	351	269	169
Platycephalus conatus	Platycephalidae	Marine, temperate	33		88	44	398	334			86	21	529	460	257	
Genypterus blacodes	Ophidiidae	Marine, temperate	28	1515	678	27	998	1615	18		311		448	438	13	
Rexea solandri[a]	Gempylidae	Marine, temperate	17	543	659	133	176	164		40	97		388	488	50	
Acanthopagrus butcheri	Sparidae	Estuarine to marine	39	738	150		1178	853		110			1498	951		

Note: 1st, primary read; 2nd, secondary read; 3rd, tertiary read.
[a]All age estimates are based on readings of whole otoliths.

or those read by an inexperienced reader are reread by an experienced secondary reader to determine intrareader precision and variability. This is indicated in Table 1, where only secondary and tertiary readings are available for some of the readers for some of the species.

Since its inception in 1991, CAF has employed more than 10 different readers. It is rarely the case that a species will be aged by only one primary reader (indicated in Table 1 by multiple readers providing the primary reads). Silver warehou is an exception; reader 2 has been the primary reader for this species since age estimates started being obtained from sectioned otoliths.

Analysis technique

The functional form used to model the probability of reader i (of I readers) assigning an animal of true age a an age of a', $P^i(a'|a)$, can be very general but needs to satisfy the constraint that $\sum_{a'} P^i(a'|a) = 1$. For example, assuming that (*i*) ageing bias depends on reader and the true age of an animal, (*ii*) the age-reading error standard deviation depends on true age and reader, and (*iii*) age-reading error is normally distributed about the expected age (i.e., the expected age given any bias in age reading) leads to the following model for $P^i(a'|a)$:

$$(2) \qquad P^i(a'|a,\varphi) \propto \exp\left[\frac{-(a' - b^i_a(\varphi))^2}{2(\sigma^i_a(\varphi))^2}\right]$$

where b^i_a is expected age when reader i determines the age of an animal of true age a, σ^i_a is the standard deviation for reader i of the age-reading error for animals of true age a, and φ is the vector of parameters that determines the age-reading error matrix.

For the analyses of this paper, the probabilities obtained from eq. 2 are set to zero for values of $a' < 0$ and larger than a prespecified maximum age. Following Richards et al. (1992) and Heifetz et al. (1998), and for illustrative purposes, the age-reading error standard deviation and ageing bias are modeled in this paper using the following three-parameter models:

$$(3) \qquad \sigma_a = \begin{cases} \sigma_L + (\sigma_H - \sigma_L)\dfrac{1 - e^{-\alpha(a-L)}}{1 - e^{-\alpha(H-L)}} & \text{if } \alpha \neq 0 \\ \sigma_L + (\sigma_H - \sigma_L)\dfrac{a - L}{H - L} & \text{if } \alpha = 0 \end{cases}$$

where σ_L is the age-reading error standard deviation for a prespecified minimum age L, σ_H is the age-reading error standard deviation for a prespecified maximum age H, and α determines the extent of nonlinearity between age and the age-reading error standard deviation and

$$(4) \qquad b_a = \begin{cases} b_L + (b_H - b_L)\dfrac{1 - e^{-\lambda(a-L)}}{1 - e^{-\lambda(H-L)}} & \text{if } \lambda \neq 0 \\ b_L + (b_H - b_L)\dfrac{a - L}{H - L} & \text{if } \lambda = 0 \end{cases}$$

where b_L is the expected age of an animal of true age L, b_H is the expected age of an animal of true age H, and λ deter-

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mines the extent of nonlinearity between age and the expected age.

The ageing techniques for which bias and imprecision are to be quantified can be based on a variety of ageing structures (including spines, otoliths, or scales). The values for the parameters that determine the age-reading error matrix for each age reader are estimated by maximizing the following likelihood function:

$$(5) \qquad L(\mathbf{A}|\boldsymbol{\beta}, \boldsymbol{\varphi}) = \prod_{j=1}^{J} \sum_{a=L}^{W} \beta_a \prod_{i=1}^{I} P^i(a_{ij}|a, \boldsymbol{\varphi})$$

where a_{ij} is the age assigned by reader i to the jth ageing structure (of J ageing structures), and $\mathbf{A}$ is the entire data set of age readings.

The βs are nuisance parameters that can be interpreted as the relative frequency of animals of (true) age a in the sample (rather than in the population from which the sample was taken). An additional term can be added to eq. 5 to make use of data for known-age animals, if such data are available (Heifetz et al. 1998). In general, not all ageing structures are read by all readers. Therefore, the likelihood function is more generally the product of eq. 5 over sets of ageing structures that were all read by the same group of readers and a separate set of βs is estimated for each such set of ageing structures.

Simulation evaluation

A simulation study is used to evaluate the performance of the approach outlined above. The aim of the simulation study was to determine how often the correct ("true") model of age-reading error is selected (which age reader is biased and the functional form for the relationship between true age and bias and that between true age and age-reading error standard deviation), as well as the extent of bias and imprecision associated with the outputs from the model.

The simulation study involved developing a true model based on one specific model of age-reading error and applying several variants of the approach outlined above to data sets that could have been observed had that "true" model been correct. Specifically, the simulation study was based on 250 replicates, each of which involves a single data set with two readers, one of whom (reader 2) produces biased age readings and both of whom make age readings subject to random age-reading error (Figs. 1*a* and 1*b*). This is equivalent to one age reader reading different structures (i.e., reader 1 could be age estimates based on sectioned otoliths, while reader 2 could be age estimates by the same reader based on whole otoliths). The true age structure of the population sampled (Fig. 1*c*) is based on the results of applying eqs. 2, 3, 4, and 5 to the data for silver warehou. The variants of the estimator considered in the simulation study are listed in Table 2. Variants 1–4 form the focus for the simulation study (variant 3 is the "true" model given the structure of the simulations), while the remaining variants form the basis for tests of sensitivity. In general, model selection criteria (such as Akaike's information criterion (AIC) and BIC) are used to select among alternative variants when the method is applied in practice, so the simulations also examine how well the BIC can select among the variants. The calculation of BIC was based on the number of parameters in the model being those of eqs. 3 and 4, as well as the number of nuisance parameters that define the true age structure of the sample. BIC was preferred to AIC (Burnham and Anderson 2002) for these simulation analyses (and when it was applied to the actual data for fish species in Australia's southern and eastern scalefish and shark fishery) because AIC tends to select the most complicated model, even when it is not the true model, because of the large number of data points.

Fig. 1. Specifications of the simulations used to evaluate the performance of the estimator of age-reading error: (*a*) ageing bias for the two readers (reader 1, solid line; reader 2, broken line), (*b*) age-reading error standard deviation, and (*c*) relative frequency of different ages in the sampled population. The solid circles in the bottom panel highlight the ages that form the focus for the results of the simulation study. The dotted lines in the upper panel indicate the 95% intervals for an age estimate for each reader.

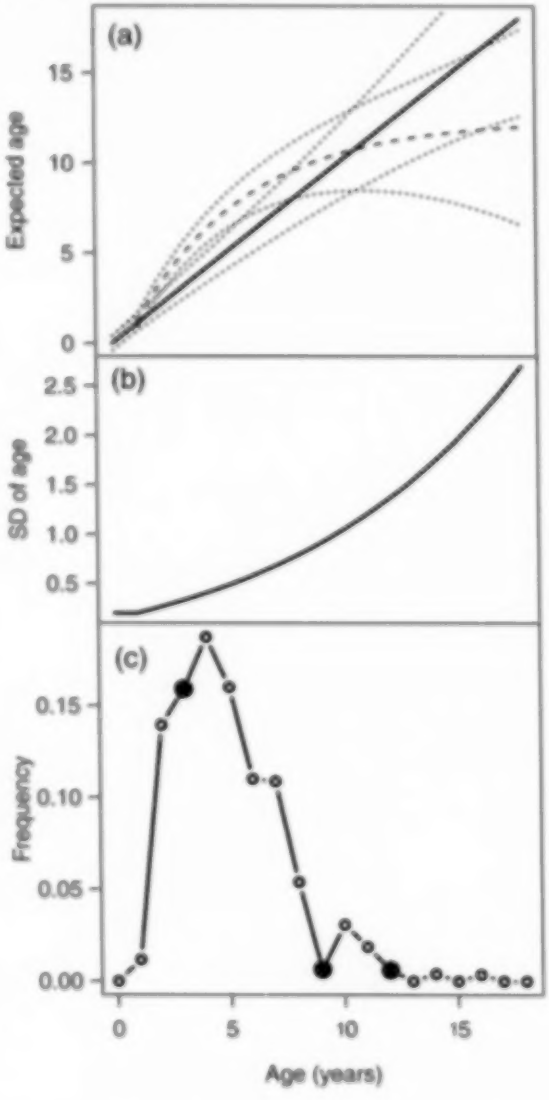

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Table 2. The eight variants considered in the simulation study.

Variant	Description
1	Both readers provide unbiased age estimates and both have the same age-reading error standard deviations
2	Both readers provide unbiased age estimates, but they differ in terms of the standard deviations of their age estimates
3	Reader 1 provides unbiased age estimates, but reader 2 is biased; both readers have the same age-reading error standard deviations
4	Reader 1 provides unbiased age estimates, but reader 2 is biased; the two age readers differ in terms of the standard deviations of their age estimates
5	As for variant 3, except that eq. 3 pertains to the coefficient of variation rather than the standard deviation
6	As for variant 4, except that eq. 3 pertains to the coefficient of variation rather than the standard deviation
7	Reader 2 provides unbiased age estimates, but reader 1 is biased; both readers have the same age-reading error standard deviations
8	Reader 2 provides unbiased age estimates, but reader 1 is biased; the two age readers differ in terms of the standard deviations of their age estimates

Fig. 2. Distributions of percent relative error for the age-reading error standard deviations for the two readers and the expected age by the biased reader. Results are shown for four estimator variants and for the variant selected using BIC. The results in this figure are based on a sample size of 500 double-read ageing structures. The quantities on the *x* axis are the age-reading standard deviations for ages 3, 9, and 12 for reader 1, the age-reading standard deviations for ages 3, 9, and 12 for reader 2, and the expected ages for ages 3, 9, and 12 for reader 2. The "true" variant for these simulations is "with bias/same SDs" (variant 3).

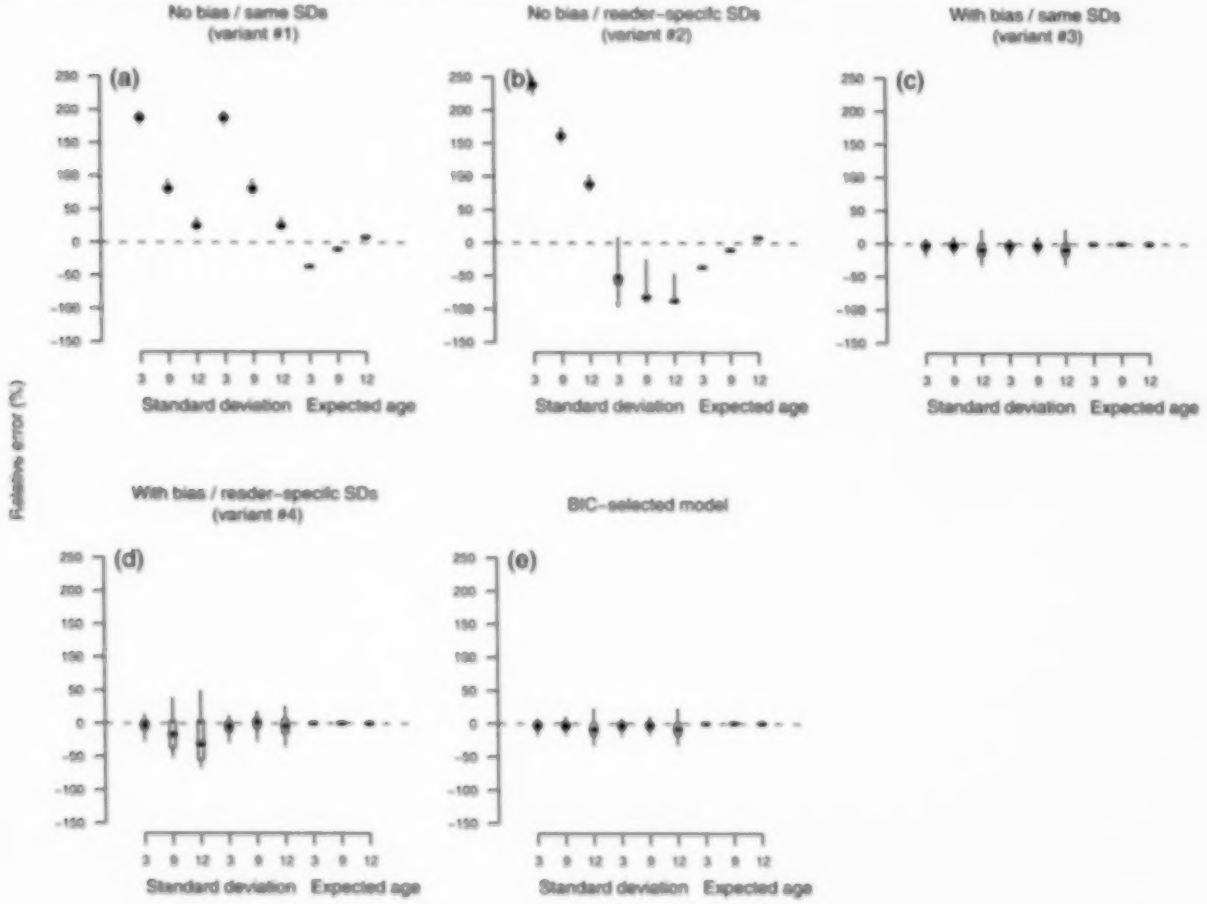

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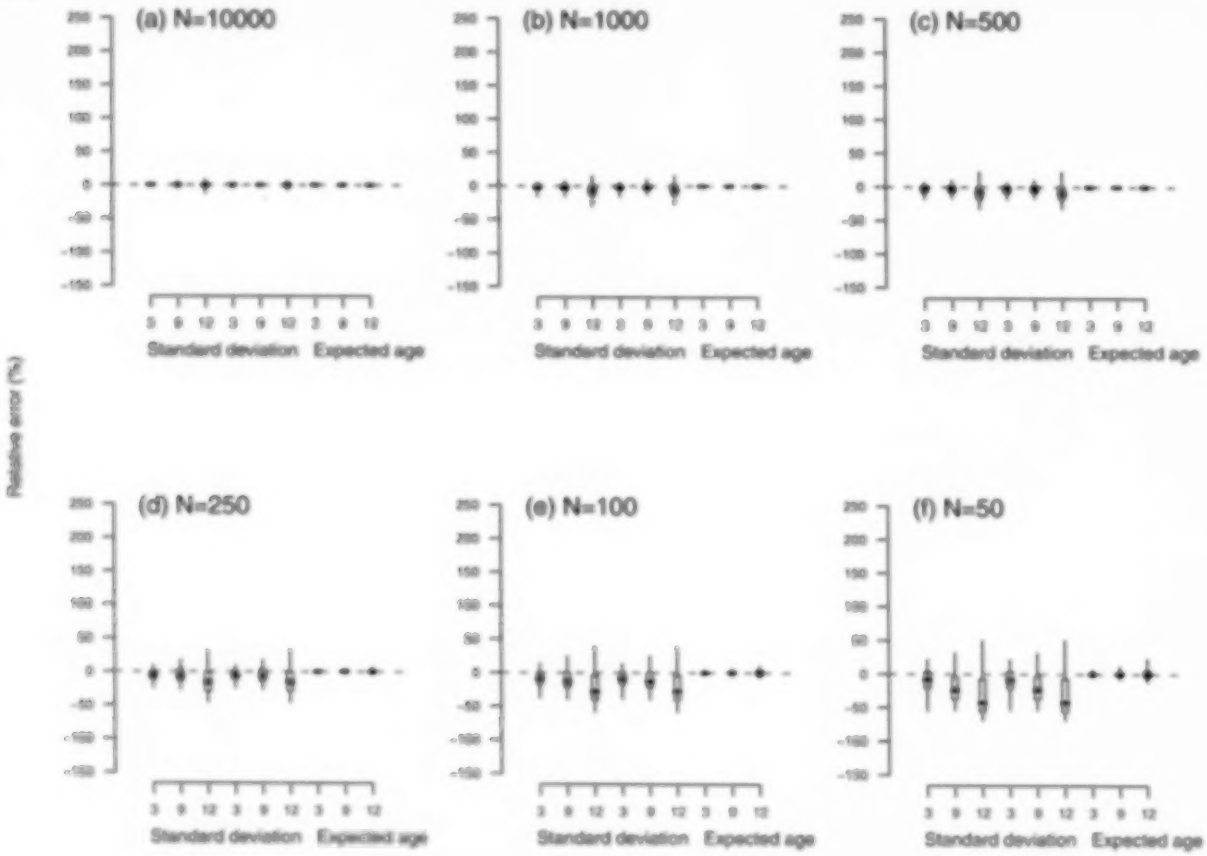
Fig. 3. Distributions of percent relative error for the age-reading error standard deviations for the two readers and the expected age by the biased reader. Results are shown for various sample sizes for an estimator that fits estimator variants 1–4 and selects a "best" variant using BIC.



The sensitivity of the results to the number of double-aged animals is examined by varying the simulated sample sizes from 50 to 10 000. Analyses were conducted in which both age readers are unbiased and in which the number of age classes is greater or smaller than those for silver warehou. The results of these simulations are not shown, however, because they were qualitatively the same as the reported results.

Results and discussion

Simulation study

The results of the simulation study are summarized by distributions of percent relative error for the standard deviations of age-reading error and for the expected ages. Ideal performance in the simulation study would involve all of the errors being zero; any systematic deviation from zero would indicate the possibility of some bias, while variability in the errors highlights a lack of precision.

The distributions of percent relative error for the standard deviations of age-reading error for ages 3, 9, and 12 (ages that are spread over the sampled population; see Fig. 1*c*), as well as for the expected ages for these ages for reader 2, suggest that assuming that the two readers are unbiased when they are not leads to estimates of both ageing bias and age-reading error standard deviations with substantial bias (Figs. 2*a* and 2*b*). This bias largely disappears when allowance is made for the possibility that reader 2 is biased. However, the estimates of age-reading error standard deviation tend to be negatively biased, particularly when allowance is made for the possibility that the age readers differ in terms of ageing imprecision (Fig. 2*d*). The results for the BIC-selected model (Fig. 2*e*) are similar to those when the true model (i.e., "with bias/same SDs") is assumed, suggesting that the BIC is capable of correctly identifying the "true" model when that model is in the set of models considered, at least for sample sizes of 500 (the "true" model was selected in over 99% of simulations).

Increasing sample sizes leads to estimates that are both more accurate and more precise (Fig. 3). However, the pattern that the estimates of the age-reading error standard deviations are negatively biased (evident in Fig. 2*e*) is exacerbated for small sample sizes. This occurs because the age-reading error standard deviations are relatively small, and for small sample sizes, almost all of the data will reflect agreement between the two age readers so there are few data

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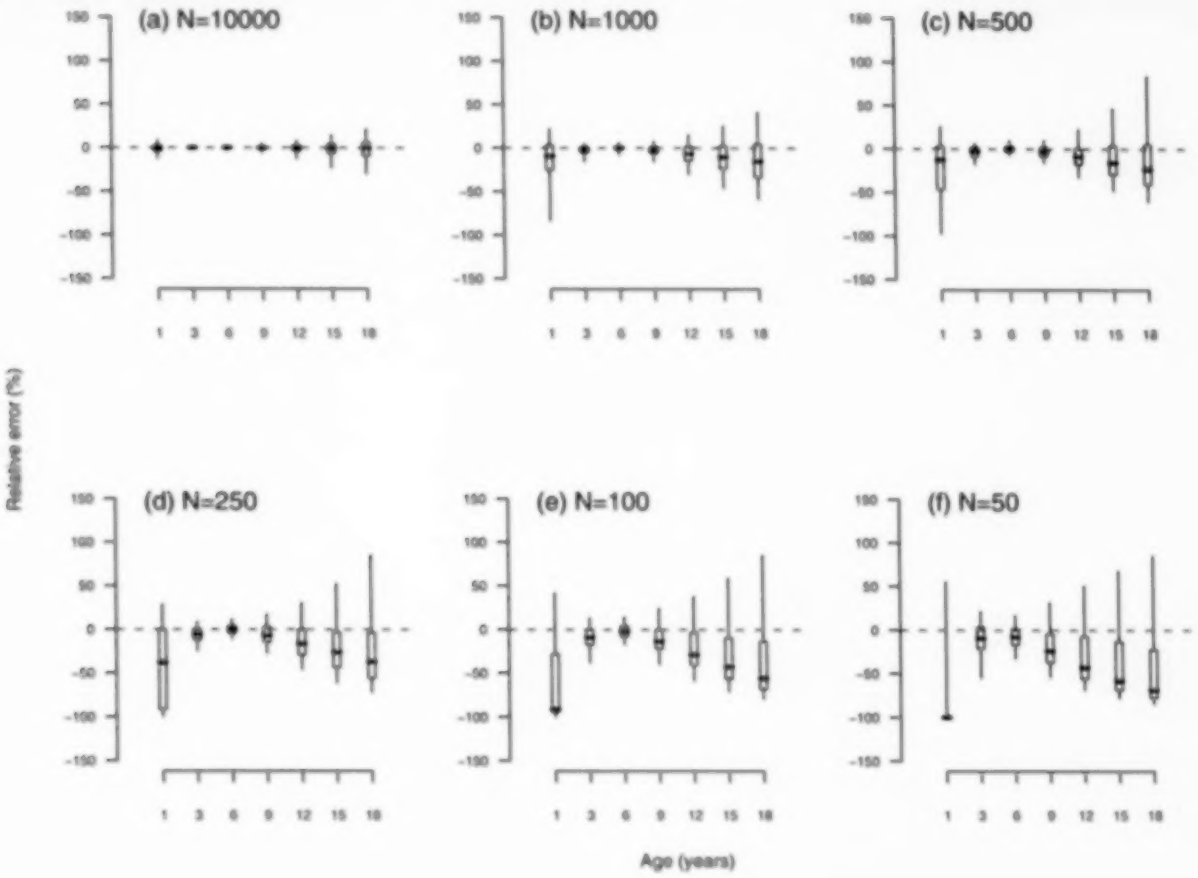
Fig. 4. Distributions of percent relative error for the age-reading error standard deviations for the biased reader (the results for the unbiased age reader are qualitatively identical). Results are shown for various sample sizes for an estimator that fits estimator variants 1–4 and selects a final variant using BIC.



to detect the magnitude of age-reading errors. The biases and poor precision for small sample sizes (evident in Fig. 3) are more substantial for ages 1, 15, and 18, ages that are poorly represented in the sampled population (Fig. 4). This occurs because unless the sample size is very large, only a few animals of these underrepresented age-classes will be included in the sample.

Although the age-reading error standard deviation is a nonlinear function of true age (Fig. 1*b*), it is possible that the data are insufficient to adequately determine the relationship between true age and the age-reading error standard deviation (particularly for small sample sizes). The estimates of age-reading error standard deviation are more precise when the coefficient of variation of age-reading error is assumed to be independent of age (variants 5 and 6) than when the age-reading error standard deviation is assumed to change with age according to eq. 3 (variants 3 and 4) (Figs. 5*c* and 5*d*). However, BIC does not select the model that visually performs best in this case (variant 5), instead generally selecting the model with different, but age-independent, coefficients of variation for the two readers (variant 6). However, the BIC-selected model outperforms the "true" model (i.e., that in which the age-reading error standard deviation increases with age according to eq. 3; Fig. 5*a*) in terms of median relative errors.

The analyses on which Figs. 4 and 5 are based assume that the biased reader can be correctly identified. Performance is (predictably) poor when reader 1 rather than reader 2 is assumed to be biased (Fig. 6). BIC is able to select the "true" model with high probability in this case, although this may be an artifact of there being some model misspecification when reader 1 is assumed to be biased.

There are two situations in which it would be anticipated that the performance of the estimator would be poor. The estimates of age-reading standard deviations are negatively biased if the age estimates are correlated (e.g., Fig. 7*b*). Furthermore, although it is possible in theory to attempt to estimate ageing bias for all readers, the estimates become very imprecise when only one of the readers is biased (contrast Figs. 7*a* and 7*c*) and imprecise and biased when both readers are biased (Figs. 7*d* and 7*e*). This poor performance is not particular to this estimator but would occur for any estimator, as the age-reading errors would be confounded. The only way to overcome the biases (Figs. 7*b*, 7*d*, and 7*e*)

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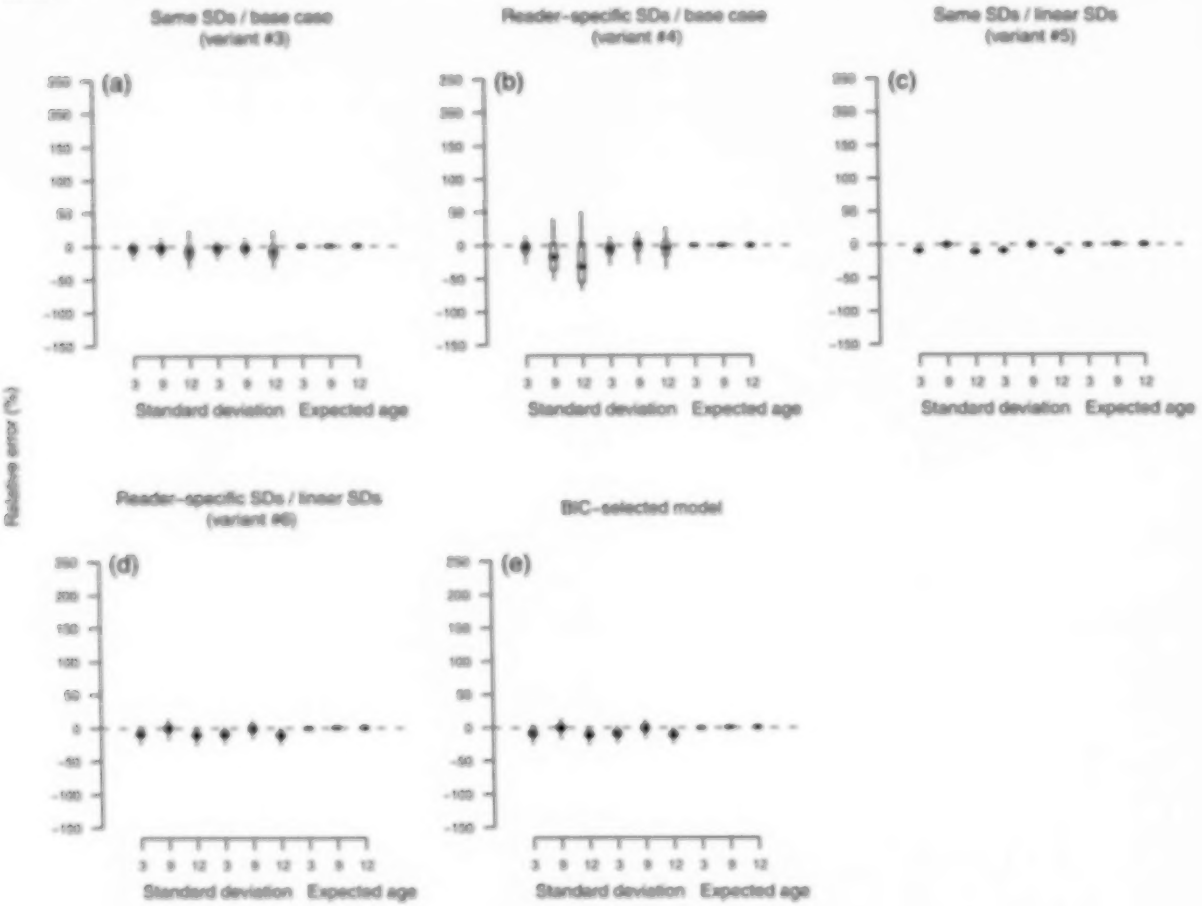
Fig. 5. Distributions of percent relative error for the age-reading error standard deviations for the two readers and the expected age by the biased reader. Results are shown for estimator variants that assume that age-reading error is governed by eq. 3 ("base case"), that assume that the coefficient of variation of age-reading error is independent of age ("linear SDs"), and for an estimator that selects among these four variants using BIC. The results in this figure are based on a sample size of 500 double-read ageing structures and the "true" model is variant 3.



would be to obtain age estimates for animals for which the true age was known.

Application to actual data

Example application: silver warehou

Silver warehou is a species (maximum age 23 years) that is distributed throughout southeastern Australia, including New South Wales, Tasmania, and Victoria. Adults of this species are found on the continental shelf and upper slope where they are one of the target species of a bottom trawl fishery (Smith 1994). Assessments of this species have been conducted using statistical catch-at-age models fitted to age and size composition information, as well as to standardized catch rates (e.g., Thomson and He 2001). The data set on which age-reading error matrices for silver warehou can be based consists of age estimates made using sectioned and whole otoliths: 1042 otoliths were read sectioned twice, 1104 were read sectioned once and whole once, and 358 were read sectioned twice and whole once. Silver warehou is therefore a fairly complicated case in which some otoliths were read three times and there are multiple methods for age determination, one of which (reading of otoliths whole) was expected to be biased.

The fits of 10 models to this data set are summarized in Table 3. Different models are considered for the first and second sectioned reads of an otolith and for the whole read of the otolith. These models examine whether the expected ages are the same for the two sectioned reads (as might be expected a priori), whether eq. 3 should relate to the standard deviation or the coefficient of variation of age-reading error, and whether it is reasonable to assume that the coefficient of variation of age-reading error is independent of age (Table 3). All of the models shown assume that age readings based on whole otoliths are biased relative to those based on sectioned otoliths and that the level of age-reading error differs between whole and sectioned otoliths (this is clearly apparent from a visual examination of the raw data).

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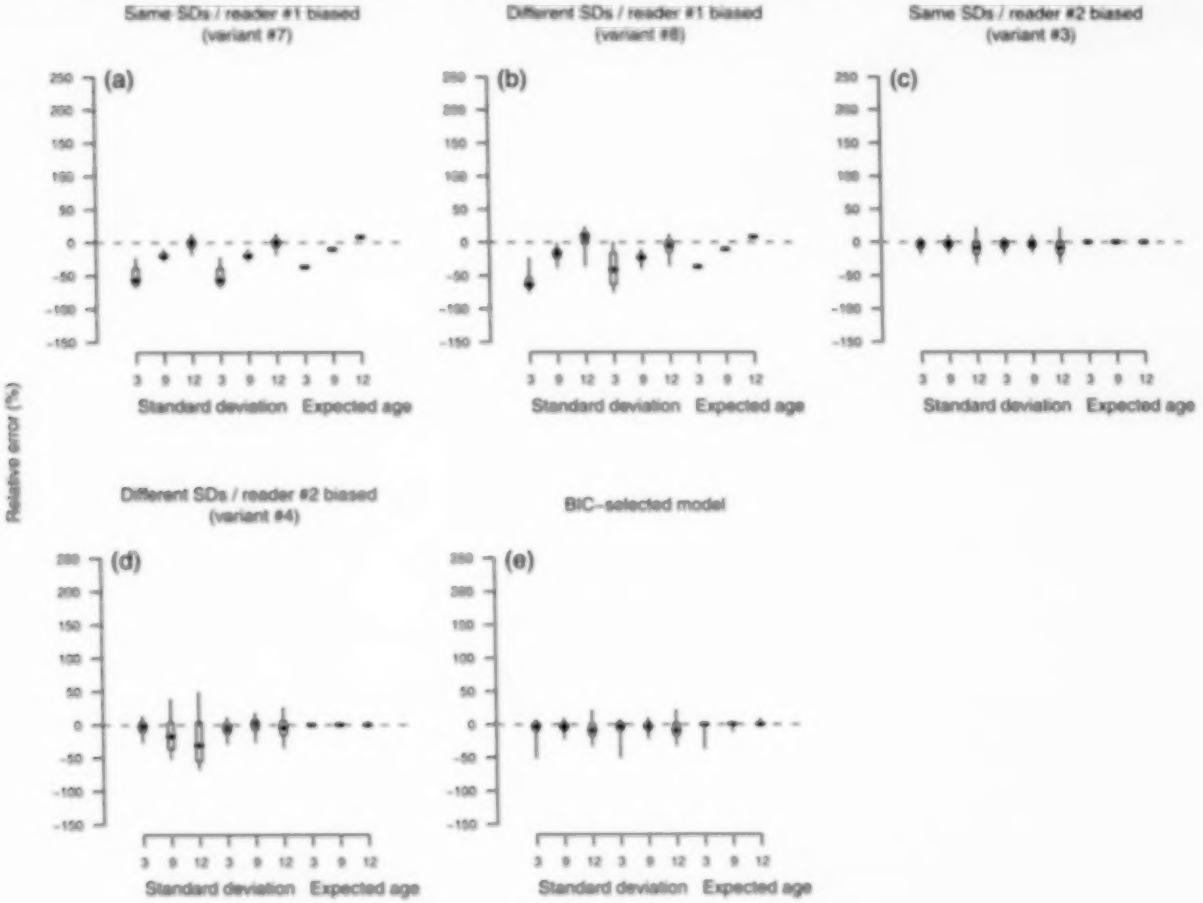
Fig. 6. Distributions of percent relative error for the age-reading error standard deviations for the two readers and the expected age by the biased reader. Results are shown for two estimator variants in which the biased reader (reader 2) is assumed to be biased (variants 3 and 4), for two variants in which the unbiased reader (reader 1) is assumed to be biased (variants 7 and 8), and for the variant selected using BIC. The results in this figure are based on a sample size of 500 double-read ageing structures and the "true" model is variant 3.



BIC selects model 9 (the two readings based on sectioned otoliths lead to the same expected ages but they differ in terms of precision). Models that assume that the two sectioned reads lead to (slightly) different expected ages and that the standard deviations of age-reading error are the same for the two sectioned reads (models 1 and 2) have BIC values most similar to that for the selected model. The models that assume that the coefficient of variation follows eq. 3 and (particularly) that the coefficient of variation is independent of age (models 5–8) have much higher BIC values than model 9. Comparing the BIC values for models 5 and 6 with those for models 7 and 8 suggests that there is very strong evidence against the assumption that the coefficient of variation for the whole readings is independent of age.

There are marked differences between the standard deviations of age-reading error for the two sectioned reads (Fig. 8*a*), with the model suggesting that the age-reading error standard deviation is much less for the second read for animals of age 6 and older. It should be noted, however, that there are very few animals of age 6 and older in the samples on which the analyses for silver warehou are based (Fig. 8*c*) and that the estimates of the standard deviations of age-reading error are imprecise for animals 10 years and older.

The APE based on sectioned readings is 3.6%, while the average coefficient of variation is 5.1%. These values are markedly lower than the coefficients of variation in Fig. 8*b*. Moreover, the use of APE or a coefficient of variation fails to indicate that the coefficient of variation of age-reading error likely changes as a function of age.

The quality of the fit of the selected model is explored, plotting the observed number of animals for each combination of age from the first sectioned read and age from the second sectioned read with the associated model prediction (Fig. 9). The fits are generally adequate (the observed and model-predicted values lie close to the 1:1 line), although the fits are poorer for combinations for which the number of observations is low. There is no evidence in Fig. 9 for overdispersion associated with the fit of model 9 (in con-

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Fig. 7. Distributions of percent relative error for the age-reading error standard deviations for the two readers and the expected age by reader 2. (*a*) Variant 3 applied when variant 3 is the true model, (*b*) as for Fig. 7*a* except that the age-reading errors are correlated (ρ = 0.71), (*c*) as for Fig. 7*a* except that ageing bias is estimated for both readers, (*d*) variant 3 applied when both age readers are biased (reader 1 positively biased, reader 2 negatively biased), and (*e*) as for Fig. 7*d* except that ageing bias is estimated for both readers. All of the results in the figure are based on a sample size of 500 double-read ageing structures.

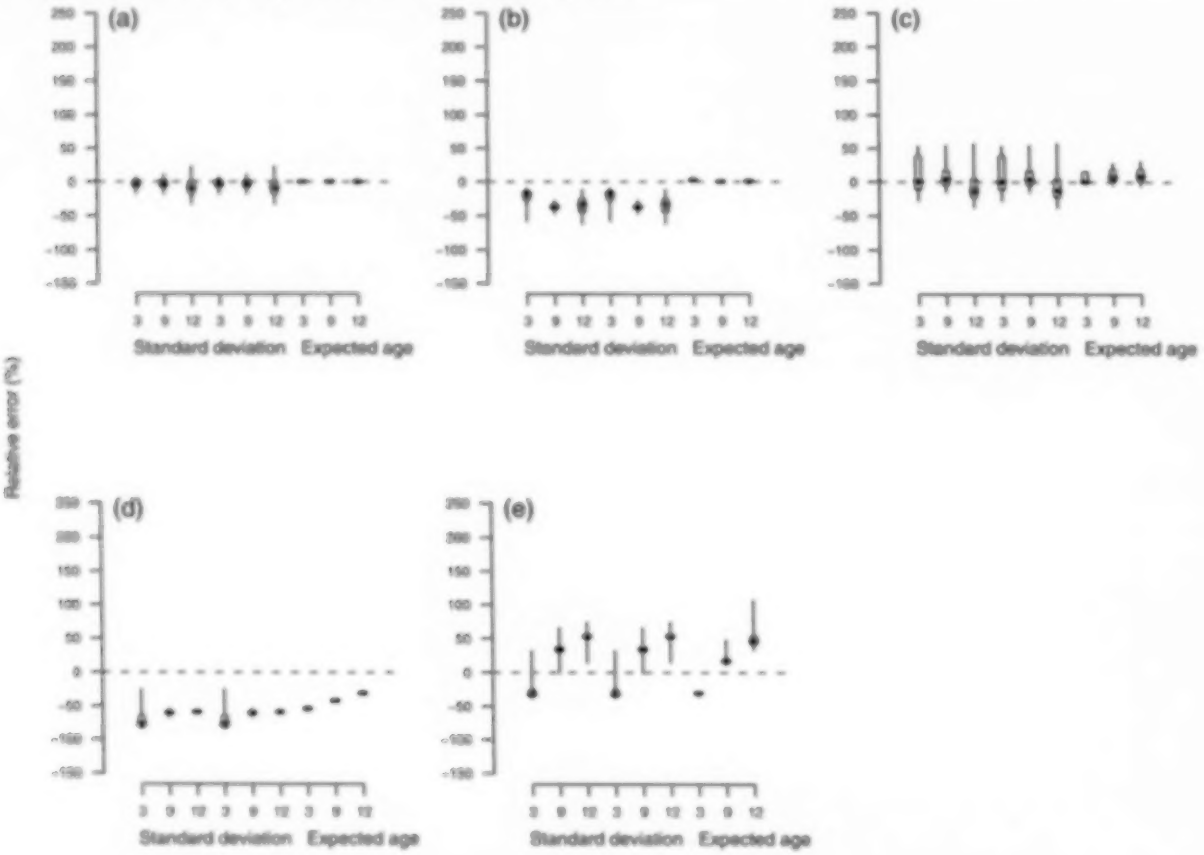

Table 3. Alternative models for age-reading error for silver warehou and the results of applying BIC to select among these models.

	First sectioned read		Second sectioned read		Whole read			
Model	Bias	Precision	Bias	Precision	Bias	Precision	No. of parameters	ΔBIC
1	Unbiased	Eq. 3	Unbiased	As for 1	Eq. 4	Eq. 3	60	7.82
2	Unbiased	Eq. 3	Eq. 4	Eq. 3	Eq. 4	Eq. 3	66	4.32
3	Unbiased	Eq. 3[a]	Unbiased	As for 1	Eq. 4	Eq. 3[a]	60	39.56
4	Unbiased	Eq. 3[a]	Eq. 4	Eq. 3[a]	Eq. 4	Eq. 3[a]	66	70.46
5	Unbiased	Con CV	Unbiased	As for 1	Eq. 4	Con CV	56	114.16
6	Unbiased	Con CV	Eq. 4	Con CV	Eq. 4	Con CV	60	106.86
7	Unbiased	Con CV	Unbiased	As for 1	Eq. 4	Eq. 3	58	14.49
8	Unbiased	Con CV	Eq. 4	Con CV	Eq. 4	Eq. 3	62	10.07
9	Unbiased	Eq. 3	Unbiased	Eq. 3	Eq. 4	Eq. 3	63	0
10	Unbiased	Eq. 3	Eq. 4	As for 1	Eq. 4	Eq. 3	63	14.36

Note: Con CV denotes that the coefficient of variation of age-reading error is assumed to be independent of age, and "as for 1" denotes that the precision of the age-reading error matrix is assumed to be the same for the two sectioned reads.

[a]Eq. 3 pertains to the coefficient of variation rather than the standard deviation.

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Fig. 8. (*a*) Standard error and (*b*) coefficient of variation of age-reading error for the three types of age readings for silver warehou (broken line, whole reads; solid and dotted lines, sectioned reads; dashed–dotted lines, asymptotic 95% confidence intervals about the point estimates). (*c*) Estimated age structures underlying the three samples for silver warehou based on the selected model.

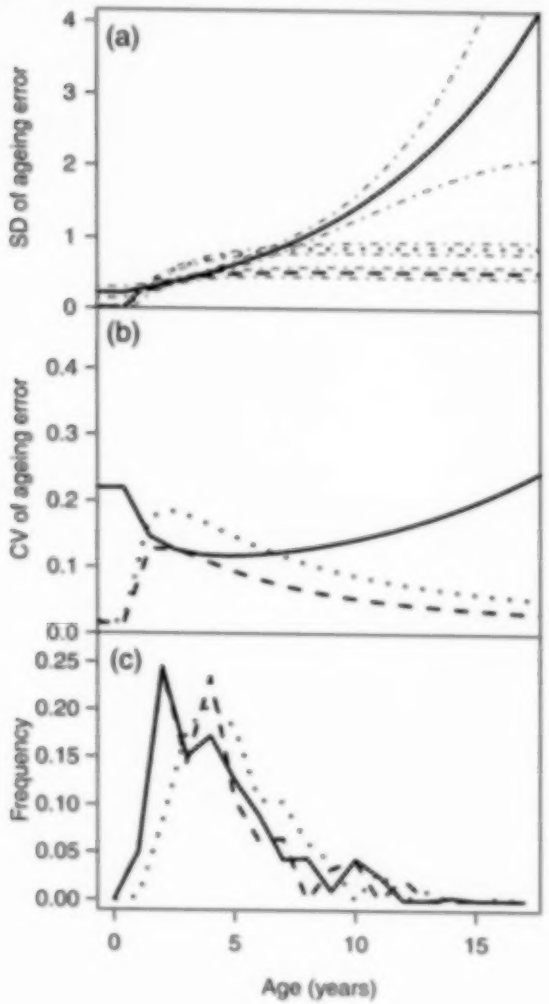
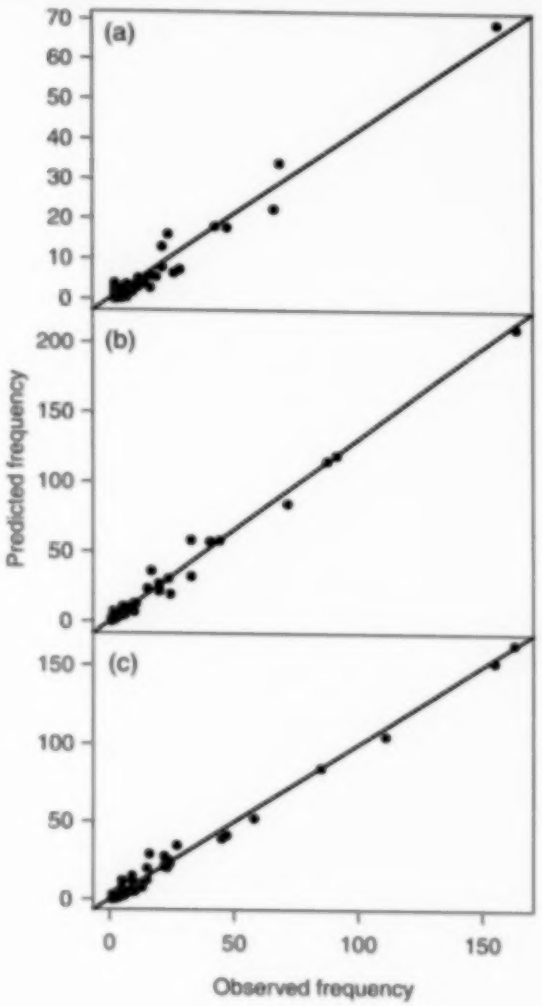


Fig. 9. Diagnostic plots for the fit of the age-reading error model to the data for silver warehou. Samples sizes for the data sets: (*a*) 358, (*b*) 1104, and (*c*) 1042.



trast, there is strong evidence for overdispersion for some of the models that led to higher BIC values than the selected model; results not shown).

Application to other species

The approach outlined above has been applied to a variety of the fish species harvested off southern Australia, and the results have been included in stock assessments based on the integrated analysis paradigm. Some of these applications are summarized (Fig. 10) in terms of the coefficients of variation and standard deviations of age-reading error as a function of true age (for the primary age reader) for seven species (the results for silver warehou are shown in Fig. 8) for a model in which all readers are assumed to be unbiased and in which the curvature parameter α (eq. 3) is estimated. This model was supported by BIC for most of the species. No plots of age versus bias are provided, as the primary reader is assumed to be unbiased.

The coefficients of variation of age-reading error decline with (true) age. The coefficients of variation of age-reading error for animals of age 2 are generally 0.12–0.20, whereas those for the oldest ages depend on species. Tiger and deepwater flathead and black bream have the lowest coefficients of variation for the oldest ages (<0.05). When expressed in terms of standard deviations, the species for which age estimates are the least precise are blue grenadier, silver warehou, and pink ling. The relationship between the age-reading error standard deviation and true age can be convex (silver warehou and blue grenadier), concave (deepwater flathead and pink ling), or asymptotic (gemfish, school whiting, black bream, and tiger flathead), highlighting the need

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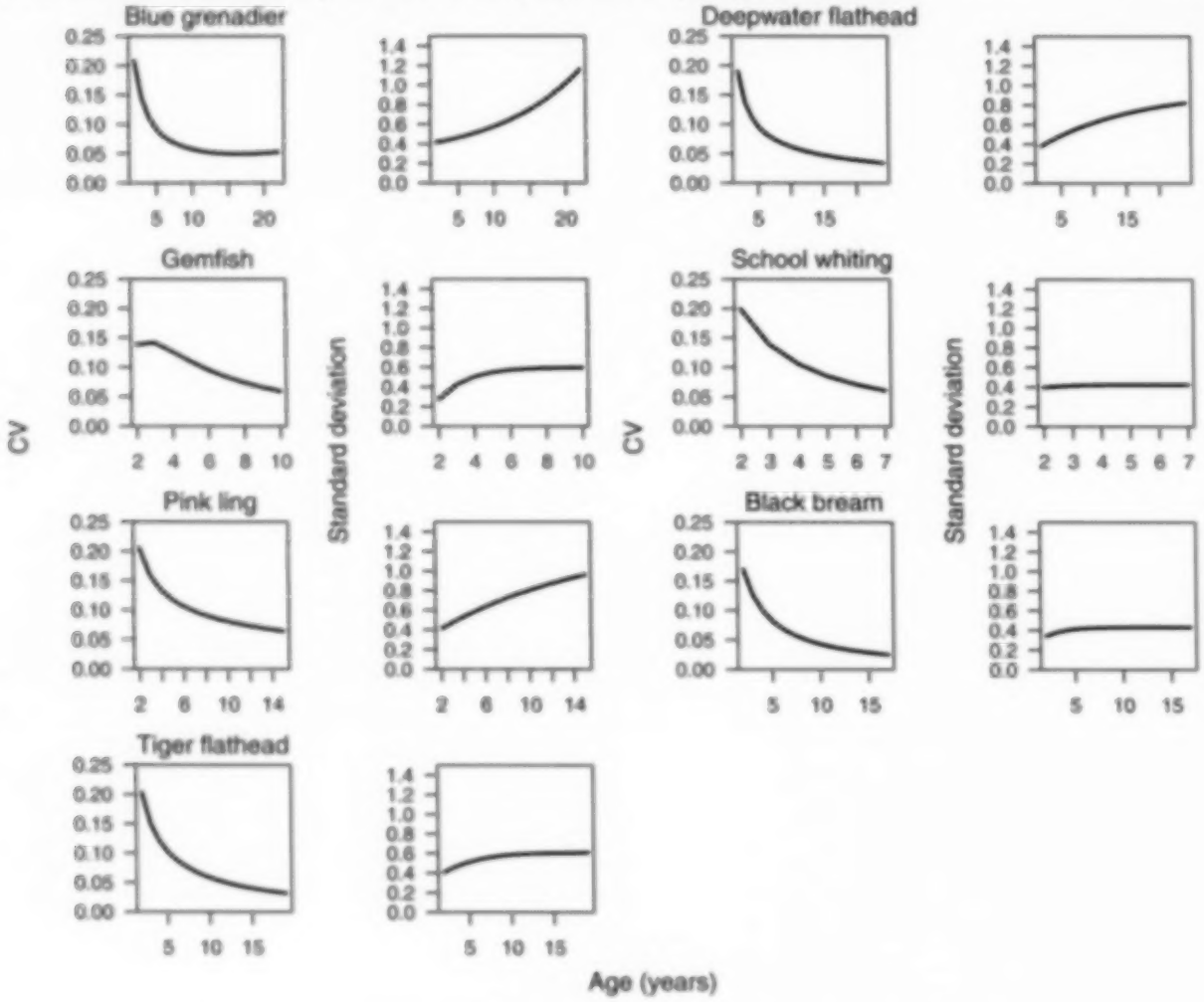
Fig. 10. Coefficients of variation (CV) and standard deviations of age-reading error versus true age for seven species in Australia's southern and eastern scalefish and shark fishery. The results in this figure pertain to the primary age reader.



to have a method for quantifying age-reading error that is sufficiently flexible to capture a wide range of alternative models of age-reading error.

General discussion

The simulation study suggests that the method is able to correctly determine both ageing bias and the extent of age-reading imprecision if sample sizes are large, particularly for those ages that are well represented in the sampled population. An implicit assumption of both the way the pseudo data sets were generated for the simulation experiment and the structure of the estimator is that age-reading errors occur at random. However, there will be correlation in age-reading errors among readers if age-reading errors are caused by factors that are common to all age-readers, i.e., misinterpretation of visual cues on, for example, an otolith or spine or due to institutional ageing protocols can lead to negatively biased estimates of the extent of age-reading error (e.g., Fig. 7*b*). Similarly, the method is unable to estimate ageing bias and age-reading imprecision when both readers are biased without auxiliary information on the true age of the sampled animals (e.g., Figs. 7*d* and 7*e*).

It is not possible to estimate the extent of correlation in age estimates among age readers and whether all of the readers are biased without auxiliary information (such as age estimates for known-age animals). Therefore, having a method that is able to estimate the extent of ageing bias and stochastic age-reading error does not replace the need for age validation using direct techniques (e.g., Francis et al. 1992; Smith et al. 1995; Kalish et al. 1997) or by tracking strong cohorts in catch-at-age matrices (e.g., Punt et al. 2001).

The estimates of recruitment for blue grenadier for analyses in which account is taken of age-reading error and in which age-reading error is assumed to be exact indicate that ignoring age-reading error leads to the sizes of weak cohorts

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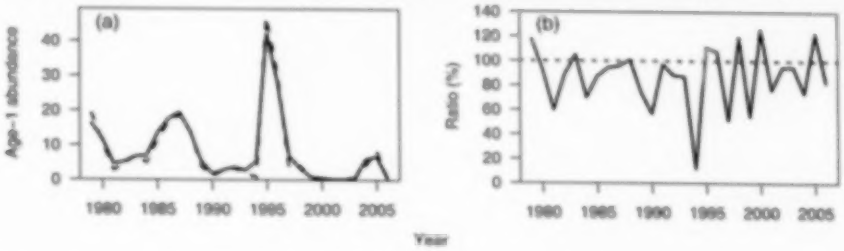
Fig. 11. (*a*) Estimates of recruitment (age-1 abundance) for blue grenadier off southeast Australia based on an assessment that accounts for age-reading error (broken lines) and an assessment that ignores age-reading error and hence assumes that the age estimates are exact (solid line) and (*b*) ratio of the estimates of recruitment accounting for age-reading error to those in which age-reading error is ignored.



being overestimated and those of strong cohorts being underestimated, with the effect that the extent of variation in recruitment is underestimated (Fig. 11). For blue grenadier at least, the size of this effect is relatively small and the general patterns of year-class strength are easily determined even if age-reading error is ignored.

The inability to account for correlations in the errors among age readers is not the only limitation of the method. The results suggest considerable variation in year-class strength for blue grenadier, and it is known that animals from the strong cohorts have grown slower than those from the weak cohorts (Punt and Smith 2001). An original aim of this work was to assess whether age-reading error was different for strong and weak cohorts of blue grenadier (an expectation being that age readers will have assigned "uncertain" otoliths to the strong cohorts; Kimura et al. 1992). However, the nature of the otolith sampling program, which is designed to provide data for stock assessment purposes, is such that the vast bulk of the samples are for the strong cohorts so that the power to detect differences in age-reading standard deviations between strong and weak cohorts is very low. The otolith sampling strategy would need to be modified considerably to address a question such as this.

Although the approach outlined above can deal with cases in which there are several readers and the data available to quantify age-reading error consist of numerous data sets in which some ageing structures are read by various subsets of the readers, this can lead to substantial computational requirements owing to the need to estimate many nuisance parameters (essentially the underlying age structure of the sample for each subset of readers). It is therefore beneficial to have a design for how double (and triple) reads are conducted and perhaps to limit the number of readers to ensure that adequate sample sizes are available for each reader. In contrast, having fewer readers may mask the ability to detect ageing bias, especially if the readers are all part of the same laboratory and hence for whom age-reading error may be correlated. It is standard practice within the CAF that only one reader is responsible for ageing a particular species each year once initial ageing protocols have been established. This should be the aim of any ageing facility that provides long-term production ageing data, although it should also be recognized that this is rarely possible due to staff turnover.

The number of double-aged animals needed to obtain relatively precise and unbiased estimates of age-reading error depends on the life history of the species (and the extent of variation in age-reading error). For example, very long-lived species would require large sample sizes. An additional problem with long-lived species is that the number of nuisance parameters depends on the number of age classes postulated to be included in the sample, so application of the estimator to long-lived species leads to fewer degrees of freedom for the same sample size, with a consequential reduction in precision. In fact, it may be appropriate to apply a rule-of-thumb such as there should be minimally a sample of 10 for each age in the sample. Finally, there are occasionally very old animals in the sample. These "loners" will impact the number of estimable parameters of the age-reading error model, and applications of the method have generally excluded the upper 1% of the oldest ages. In principle, the difficulties associated with "loners" and long-lived species could be overcome by implementing the estimation method within a random effects context. Unfortunately, the nuisance parameters (which would constitute the random effects in a random effects model) enter the model in a highly nonlinear way, rendering the problem of maximizing the likelihood function computationally prohibitive at present. It is possible that Bayesian methods (based, for example, on the WinBUGs platform) could be used to overcome the computational concerns associated with a nonlinear random effects implementation of the method.

A variety of techniques, both numerical and graphical (e.g., Beamish and Fournier 1981; Campana 2001; Power et al. 2006), have been developed to examine age-reading error. Some of these (e.g., the "percent agreement" method) are now known to be inappropriate in many contexts (Campana et al. 1995), whereas others (e.g., computing an age-reading error coefficient of variation) are based on a specific model of age-reading error (in this case, that age estimates are random and unbiased with a constant coefficient of variation). In the past, age-reading error matrices based on age-bias tables have formed the basis for assessments (e.g., Smith and Punt 1998; Punt et al. 2001). The estimator outlined above implicitly includes several of the previous methods for quantifying age-reading error as special cases. The basic approach (i.e., eqs. 3 and 4) can be extended to include a wider set of models without negatively impacting the basic analytical structure. This flexibility, combined with the use of model selection methods such as BIC, permits the selection of an appropriate model for age-reading error for each specific case.

Clark (2004) outlined a nonparametric approach for quan-

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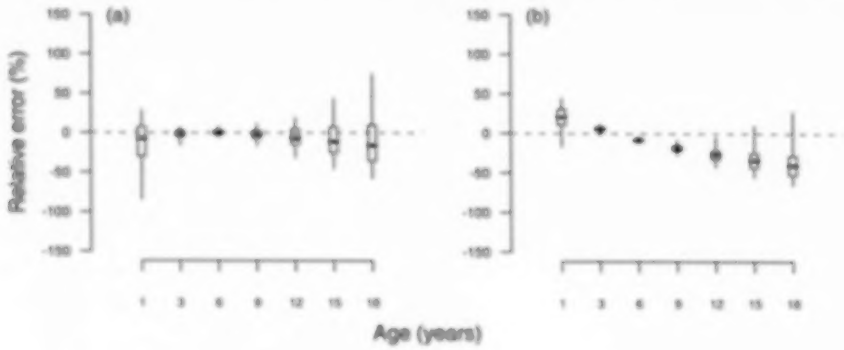
Fig. 12. Distributions of percent relative error for age-reading error standard deviations based on (*a*) the method in this paper and (*b*) that of Heifetz et al. (1998) in which the "true" age for an otolith is set equal to the average of its two age estimates. The sample size for this figure is 500.



tifying ageing precision. This approach, being nonparametric, is very flexible. However, to provide precise estimates, it requires very large sample sizes, much larger than those that are typically available in actual applications. In addition, the method only provides unique estimates if the distribution for age-reading error is assumed to be symmetric. The original method of Richards et al. (1992) did not treat the true ages as random variables but rather set them to the modal value across age estimates. Similarly, Heifetz et al. (1998) set the true age equal to the average age estimate. The method of this paper is compared with that applied by Heifetz et al. (1998) for a case in which there is one age reader and it is known that the age reader is unbiased (i.e., variant 1; Fig. 12). There is a tendency for both methods to provide negatively biased estimates of age-reading standard error, but the approach of this paper is much closer to being unbiased than that of Heifetz et al. (1998).

Although the method of Richards et al. (1992), as modified in this paper, provides a better basis for estimating the entries of age-reading error matrices, simpler methods such as APE, coefficients of variation, and age-bias plots continue to play an important role in ageing programs. Specifically, these methods provide a rapid (and easily understood) way to ensure quality control in ageing laboratories, such as Australia's CAF, and there is no reason that they should not continue to be used for this purpose. However, the number of rereads needed to apply these methods, given their largely qualitative use, can be much less than is needed to provide reliable estimates of the entries of age-reading error matrices. Adoption of methods such as that outlined in this paper to provide the types of input needed for stock assessment purposes implies (generally) an increase in the number of rereads conducted routinely, although the number of rereads could be minimized by selecting otoliths for rereading to ensure a relatively uniform coverage of the ages for which measures of age-reading error are most needed. Fairly regular calculation of age-reading error matrices using the method in this paper will also provide a stronger (and more quantitative) basis to evaluate whether the ageing procedures remain consistent over time. Finally, consideration needs to be given to the trade-off between conducting double reads to enable age-reading error matrices to be estimated and conducting primary reads to ensure that the data necessary for stock assessment purposes (e.g., the construction of catch age compositions and age–length keys) are of sufficient precision. In principle, this trade-off could be evaluated by means of simulations that capture the entire management system, including data collection schemes, data analysis (such as construction of age–length keys and ageing error matrices), and application of stock assessment methods and harvest control rules.

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Habitat quality enhances spatial variation in the self-thinning patterns of stream-resident brown trout (*Salmo trutta*)

Javier Lobón-Cerviá

Abstract: This study explored the extent to which variation in habitat factors related to growth and density influence self-thinning patterns in stream-living brown trout (*Salmo trutta*). Analysis of 110 cohorts at 12 sites of four contrasting streams revealed density–mass relationships in two phases. Density of survivors decreased little during the first half of their lifetime. A second phase commenced as individuals attained a threshold mass upon which density declined linearly with increased mass. The slopes of the second phase were greater than predicted by space and food demands. Among sites, these slopes were related to threshold densities at the beginning of the second phase. In turn, elevations, threshold densities, and slopes depicted concave trajectories against site depth, whereas threshold masses increased linearly. Apparently, cohorts remain below the carrying capacity during the first half of their lifetime and self-thin during the second half. Space-limited habitats impose site-specific carrying capacities and site-specific self-thinning coefficients, suggesting a common mechanism underlying self-thinning and an unanticipated, emerging property: two-phase patterns with far more variation in self-thinning coefficients. Variability in growth and density exhibited by brown trout and other salmonids across regions suggests that two-phase patterns may occur broadly, and self-thinning coefficients may vary widely.

Résumé : La présente étude explore dans quelle mesure la variation des facteurs de l'habitat reliés à la croissance et la densité influence les patrons d'auto-éclaircie chez des truites brunes (*Salmo trutta*) vivant en eau courante. L'analyse de 110 cohortes à 12 sites dans quatre cours d'eau bien différents indique deux phases dans les relations densité–masse. La densité des survivants diminue peu durant la première moitié de la vie des poissons. Une deuxième phase débute lorsque les individus atteignent une masse seuil au-delà de laquelle la densité diminue en fonction linéaire de l'accroissement de masse. Les pentes de cette seconde phase sont plus fortes que ne permettent de le prédire les besoins en espace et en nourriture. Parmi les sites, ces pentes sont reliées aux densités seuils au début de la seconde phase. En séquence, l'altitude, la densité seuil et la pente décrivent des trajectoires concaves en fonction de la profondeur du site, alors que la masse seuil augmente de façon linéaire. Il semble que les cohortes demeurent sous le stock limite durant la première moitié de leur cycle et procèdent à une auto-éclaircie durant la seconde moitié. Les habitats limités en espace imposent des stocks limites et des coefficients d'auto-éclaircie spécifiques au site, ce qui laisse croire à un mécanisme commun sous-jacent à l'auto-éclaircie et une caractéristique émergente inattendue, soit des patrons biphasiques avec beaucoup plus de variation dans les coefficients d'auto-éclaircie. La variabilité de la croissance et de la densité observée chez la truite brune et d'autres salmonidés dans les diverses régions indique que les patrons biphasiques peuvent se produire sur une grande échelle et que les coefficients d'auto-éclaircie peuvent varier considérablement.

[Traduit par la Rédaction]

Introduction

The importance and implications of body size to the structure and dynamics of populations composed of individuals with indeterminate and flexible growth have been well documented (Peters 1983; Lomicki 1988). Self-thinning refers to the allometric relationship between density (N) and body size (W) caused by intraspecific competition when a crowed population reaches the carrying capacity of the habitat. This relationship takes the form $N = aW - b$ or

$$(1) \quad \log(N) = a - b\log(W)$$

Self-thinning is the ultimate expression of competition for limited resources and eq. 1 relates density and mass to define the carrying capacity of the habitat. In eq. 1, the significance of the intercept (a) is uncertain but is likely related to the habitat quality, whereas the slope (b) is the self-thinning coefficient and is thought to be determined by the demands of space and food. Following studies by Yoda et al. (1963) on intraspecific competition among higher plants, substantial evidence has been presented in support of this rule in sessile (Damuth 1998) and mobile (Fréchette and Lefaivre 1995) organisms, including invertebrate species (Begon 1986; Latto 1994; Guiñez et al. 2005) and vertebrate populations of birds (Juanes 1986), mammals (Silva and Downing 1995), and fishes (Grant 1993; Steingrímsson and Grant 1999). In addition, experimental studies on fishes

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have corroborated these patterns (Dunham et al. 2000; Keeley 2003).

As expected, based on the allometric relationship between density and mass, in populations of stream-living salmonids, individuals that are actively growing increase their rate of feeding and spatial demands. Therefore, all other things being equal, the number of growing individuals that a stream may support declines with a corresponding increase in the size of fish (Grant 1993). Several studies have suggested that in these populations, the slope of self-thinning should decline and track the metabolism and food consumption rates that scale to either (*i*) body mass by exponents 0.87 and 0.73, respectively (Keeley and Grant 1995; Keeley and McPhail 1998; Steingrímsson and Grant 1999) or (*ii*) territory size that scales to body mass by an exponent of 0.86 (Grant and Kramer 1990; Keeley 2003).

Nevertheless, the results of relevant studies have offered a variety of self-thinning coefficients. Instances in which density appeared unrelated to mass were reported by Dunham and Vinyard (1997), whereas other observational (Elliott 1993; Grant 1993; Bohlin et al. 1994) and experimental (Keeley 2003) studies described linear trends consistent with the monotonic line defined in eq. 1. Moreover, Lobón-Cerviá and Mortensen (2006) recently described density–mass relationships with two phases of markedly different self-thinning slopes for three geographically disjunct populations of resident, sea-migratory, and lake-dwelling brown trout (*Salmo trutta*). In this study, negligible declines in density with increased mass during an early phase suggested that those populations were below the carrying capacity during a prolonged time period that lasted for the first half of their lifetime. For the second half of their lifetime, these populations self-thin when space becomes limited and competition for space imposes severe density-dependent mortality (Rincón and Lobón-Cerviá 2002; Lobón-Cerviá and Mortensen 2006). Across studies, however, similarity among the exponents of metabolism (0.87), food consumption (0.73), and territory size (0.86) precluded the elucidation of the exact mechanism underlying those patterns.

Clearly, if the self-thinning rule is to be considered a general phenomenon in stream salmonids and is to be used in the management of these populations (Armstrong 2005), it is critical to identify the conditions under which these populations self-thin, the shape and slope of these relationships, and whether common mechanisms underlie these relationships. A better understanding of the drivers of population-level responses to habitat quality may reveal the underlying mechanisms.

Most studies have assumed a null hypothesis of no effect from habitat factors related to growth and density on the self-thinning patterns, which is a major prediction from the invariant self-thinning rule described in eq. 1. Nevertheless, the two-phase patterns emphasized that self-thinning coefficients differed among populations and among cohorts and were typically greater than those predicted by the food and space demands (Lobón-Cerviá and Mortensen 2006).

In the present study, I explored whether habitat characteristics related to growth and density along environmentally heterogeneous stream gradients affected the occurrence and shape of self-thinning patterns in stream-resident brown trout. For this analysis, the data set included the measurement of growth, density, and environmental factors at 12 sites of four stream tributaries of Rio Esva (northwestern Spain), where previous studies indicated temporally persistent variations in growth and density across spatial scales (Lobón-Cerviá 2004, 2007). I examined long-term trends in the relationship between density and mass during the whole lifetime of 110 cohorts and explored (*i*) whether the decline in density with increased mass followed the two-phase patterns previously described for populations at broader geographical scales and (*ii*) whether the slopes of the density–mass relationships actually reflect self-thinning. Specifically, I compared the slopes of the density–mass relationships with the predictions from food and space demands to evaluate whether departures from the predicted values were influenced by site-specific population traits (e.g., growth and density) and (or) by factors related to habitat quality. (*iii*) Lastly, as a consequence of these potential traits and habitat factors, I evaluated whether the mechanism underlying self-thinning was common across streams and sites.

Material and methods

Study area

This study was completed in four tributaries of the Rio Esva drainage (Asturias), one of the numerous coastal drainages of the 700 km long Cantabrian corridor of northwestern Spain, the waters of which flow north to open into the Cantabrian Sea. The Rio Esva drainage (~500 km^2) contains a complex net of low-altitude streams fed by rainfall and runoff. From the sources at about 800 m above sea level, rapid and well-oxygenated waters flow across rugged and deep, forested valleys over quartzite bedrock. Along the streams, patches of abundant riparian forest alternate with grass meadows. Thus, sites along streams may vary from fully covered by overhanging vegetation to completely unshaded sites in open meadows. These features combine with abundant reproductive and feeding habitats over gravel, pebble, and boulder dominated substratum to offer optimal conditions to meet brown trout requirements (Armstrong et al. 2003).

The streams and sites were selected to include the environmental heterogeneity and variability in trout densities across the Rio Esva landscape (Lobón-Cerviá 2004). Accordingly, the study sites were selected to include a run–riffle–pool sequence and variation in channel size, structure, and canopy and to be of a size (length 60–80 m, width 2–10 m, and mean depth < 0.5 m) to maximize the accuracy of population estimates (Lobón-Cerviá 2004). The 12 study sites were scattered along four subdrainages, two of which flow in an east–west direction towards the main stem of Rio Esva and the other two flow in the opposite, west–east direction. In turn, the streams and sites are representative of the numerous streams flowing north and south across the Cantabrian corridor. The streams and sites of this study are as follows: Rio Chaballos, four sites (Ch1 to Ch4); La Viella, three sites (V5 to V7); Castañedo, three sites (C8 to C10); Choudral, two sites (Cho11 and Cho12). Further details can be found in Lobón-Cerviá (2004, 2007).

Data collection and the brown trout populations

Collection methods and sampling routines have been

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described in detail elsewhere (Lobón-Cerviá 2004, 2007); therefore, only features relevant for this study are included here. At least three monitoring censuses per year (January, May, and September) were conducted since 1986 at sites Ch1, Ch2, and Ch4 of Rio Chaballos, since 1988 at site Ch4 of Rio Chaballos, and since 1989 at all other sites of Rios La Viella (V5, V6, and V7), Castañedo (C8, C9, and C10), and Choudral (Cho11 and Cho12). Brown trout size and numbers were quantified with electrofishing techniques by applying the three-pass removal method (Lobón-Cerviá 2003). All samples were conducted under baseflow conditions. After each sample, detailed bathymetric maps were drawn and the corresponding environmental variables were recorded. Densities were calculated separately for age-0, age-1, and older individuals and are referred to the site area calculated from the bathymetric maps. No detectable difference in daily temperature among streams led to the assumption that all brown trout experience the same temperature regime at the 12 sites and differences in growth were primarily the result of other factors (i.e., food availability; Lobón-Cerviá and Rincón 1998).

This study encompasses 110 cohorts emerging in the years 1986 to 1998. The size and density of each cohort and site was quantified, on average, 10 times from recruitment until the time of complete disappearance. Peak emergence occurred over approximately the same dates throughout the river drainage, though it varied slightly among years; thus, for practical purposes, I assumed the same population birth date as 15 March for all cohorts and sites. The maximum age for every cohort and site was assumed to be the age (in days since birth date) of the individuals in the samples just before the complete disappearance of the cohort. Life span was more variable among sites than among cohorts, within an overall range of 900–1200 days.

Data analysis

I analyzed cohort dynamics using a nested design (sites within streams). To assess differences in cohort density and growth among streams and sites, I calculated the mean density (N_M, individuals·m^{-2}) and the mean mass (W_M, g) averaged from recruitment through the lifetime to the total disappearance of each cohort and site and compared these measures using a nested analysis of variance (ANOVA; Zar 1984).

To explore the prediction that survivor density declined with increased mass, i.e., the potential self-thinning relationships, I examined the trajectories depicted by the $\log_{10}$-transformed survivor density (D, individuals·m^{-2}) versus body mass (W, g) as single observations. Visual inspections of these trajectories suggested a predominance of distinctly nonlinear trends characterized by an early phase with shallow or negligible slope followed by a second phase of markedly steeper slope. Therefore, I explored the suitability of the monotonic line of eq. 1, $N = A + BW$, relative to a two-phase regression in the form

$$(2) \qquad N = A_1 + B_1W(W \leq K) + A_2 + B_2W(W > K)$$

where N and W are the log-transformed density and mass, respectively, A, A_1, and A_2, the elevations, and B, B_1, and B_2, the slopes. Relative to the continuous decline of eq. 1, the two-phase model of eq. 2 contains a restriction for continuity at the break point K and density changes of direction at $A_1 + B_1K = A_2 + B_2K$. For computational purposes, eq. 2 can be rewritten as

$$N = A_1 + B_1W(W \leq K) + [A_1 + (B_1K + B_2K + WK)](W > K)$$

This reformulation offers the advantage that only one elevation (A_1) and the two slopes of the shallow and steep wings (B_1 and B_2) needed to be estimated. Once the density–mass lines were established, I tested their slopes against the coefficient of the territory size and food consumption hypothesis (i.e., 0.87).

The major objective of this study was to explore the effects of site-specific environmental factors (i.e., extrinsic factors) and relevant population traits (i.e., intrinsic factors) on the density–mass patterns. These patterns depicted distinctly nonlinear trajectories characterized by an earlier, nonsignificant phase followed by a second phase of severe decline (see Results). Therefore, I focused this exploration on the interactions among the following intrinsic factors: (*i*) the elevations that represent the average recruitment across cohorts, (*ii*) threshold masses and threshold densities at which the trajectory changed direction, (*iii*) the slopes of the second phase, and (*iv*) growth during the second phase. As a proxy of the growth experienced by individuals when the cohorts are self-thinning, I used the mean mass of the individuals (W_K, g) attained during the second, steep phase that corresponds to the second half of the lifetime. As a major factor extrinsic to the population, I explored the effects of site depth as a proxy of the space available at a site scale. These site depths were quantified as the mean depth of the sites calculated on the bathymetric maps drawn after each sample; depths were measured every 1 m across transects every 10 m along the study site.

Results

Spatiotemporal variations in growth and density

The cohorts varied widely in density and growth among sites and streams (Fig. 1). A hierarchically nested design revealed no significant difference in the mean cohort density among streams ($F_{[3,8]} = 0.86$, $p = 0.49$) but highly significant differences among sites ($F_{[8,96]} = 11.5$, $p < 0.001$) and among cohorts ($F_{[12,96]} = 12.9$, $p < 0.001$) and highly significant differences in the mean cohort mass among streams ($F_{[3,8]} = 12.1$, $p = 0.002$), among sites ($F_{[8,96]} = 10.1$, $p < 0.001$), and among cohorts ($F_{[12,96]} = 1.87$, $p = 0.04$).

Brown trout showed persistently faster (Ch1, Ch2) or persistently slower (Cho11, Cho12) growth at a few sites. Also, density showed a trend to be site-specific, with some sites showing persistently low density and little variation among cohorts (Ch4) relative to other sites where density was persistently higher (Ch3) and varied substantially among cohorts (Ch2, V6). Thus, patchiness across sites was expressed in combinations of growth and density with sites where trout showed persistently low density and slow growth, high density and fast growth, and intermediate density and growth. These among-site differences in growth and density persisted over the study years (Fig. 1).

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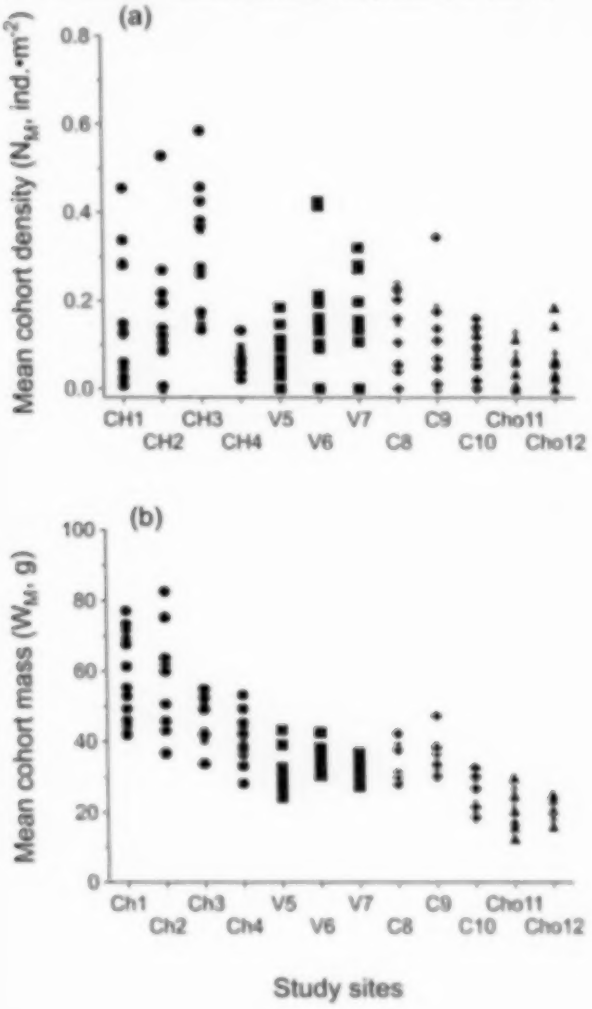
Fig. 1. Variation in the density and growth of the cohorts analyzed across streams and sites: (*a*) mean cohort density (N_M, individuals (ind.)·m^{-2}) and (*b*) mean cohort mass (W_M, grams) averaged across samples conducted every 4 months from recruitment to the complete disappearance of 110 cohorts of brown trout (*Salmo trutta*) at 12 study sites of Rio Chaballos (Ch1–Ch4), La Viella (V5–V7), Castañedo (C8–C10), and Choudral (Cho11–Cho12) (Rio Esva drainage, northwestern Spain). The numbers of cohorts examined at each site and other related information are presented in Table 1.



Density–mass relationships

The trajectories depicted by log-transformed density–mass relationships for each of the 110 cohorts highlighted an overwhelming predominance of two-phase patterns. The first phase commenced at recruitment, and the density of survivors remained practically unchanged during a prolonged time period of increasing mass that lasted for the first half of the lifetime. A given mass attained by individuals signaled the onset of the second phase, in which density declined steeply with increased mass and continued to decline until the total disappearance of the cohort (Fig. 2).

The Akaike information criterion (AIC; Akaike 1973) indicated a 99.9% probability (ΔAIC_1 = 26–103) that a two-phase regression was the best model to fit all instances, relative to a single linear regression. The corresponding fits of two-phase regressions for each single site (cohorts pooled) were all highly significant and revealed that 60.8%–89.6% of the variations in survivors density could be explained by variation in fish mass (Table 1). For streams (sites pooled) and for the whole data (streams and sites pooled), the variations in density explained by variations in fish mass attained 60.4%–81.3% and 58.7%, respectively (Table 1).

Analyses of covariance (ANCOVAs) revealed highly significant differences among elevations ($F_{[11,382]}$ = 11.6, $p < 0.001$) for the 12 regressions of the first phase and highly significant differences among elevations ($F_{[11,548]}$ = 7.41, $p < 0.001$) and among slopes ($F_{[11,548]}$ = 5.37, $p < 0.001$) for the 12 regressions of the second phase. In addition, the regressions of the second phase among streams (pooled sites) showed highly significant differences among elevations ($F_{[3,564]}$ = 4.67, p = 0.03) and among slopes ($F_{[3,564]}$ = 5.34, p = 0.001), indicating relevant effects of site-specific or stream-specific factors on the coefficients of the density–mass relationships. Moreover, the Akaike information criterion applied to the suitability of the slopes of the second phase relative to the exponents for which the metabolic rate and territory size scale to body mass (i.e., 0.87) revealed a 99.5% probability (ΔAIC_2 = 11–57) that the two-phase fits with unconstrained slopes were the best fit to the data.

Consequently, two-phase regressions suitably described the density–mass relationships for the 12 sites, four streams, and whole data set. Coefficients of the two-phase regressions, including elevations, threshold masses, threshold densities and biomasses, and the two slopes of the shallow and steep phases, are shown (Table 1). In these two-phase patterns, the slopes of the first phase were only significant at two sites (Ch3 and V6) and attained magnitudes (0.35 and 0.44, respectively) markedly lower than the predictions from the food and space demands (i.e., 0.87). In contrast, all slopes of the second phase were highly significant and substantially greater (range 1.54–2.62; Table 1) than the exponents predicted by the food and space demands. Moreover, differences among sites in the coefficients of these relationships (Table 1) were also reflected in differences in elevation, representing the mean recruitment across cohorts (range among sites 0.13–0.86 individuals·m^{-2}) and in the threshold masses (range among sites 12.4–37.2 g·individual^{-1}). Interestingly, given substantial differences in growth among sites, the time needed to attain these threshold masses varied between 450 and 750 days, a difference of almost a year in the commencement of the second, steep phase, depending on the site.

Density–mass coefficients in relation to intrinsic factors

Comparison of the interactions between factors intrinsic to the populations and density–mass coefficients across sites highlighted that even if the slopes of the first phase were only significant in two sites (i.e., Ch3 and V6), a plot of these slopes (B_1) against the elevations (A_1) showed a significant trend to increased slopes with increased elevations (r^2 = 0.48, p = 0.01), indicating a greater mortality during

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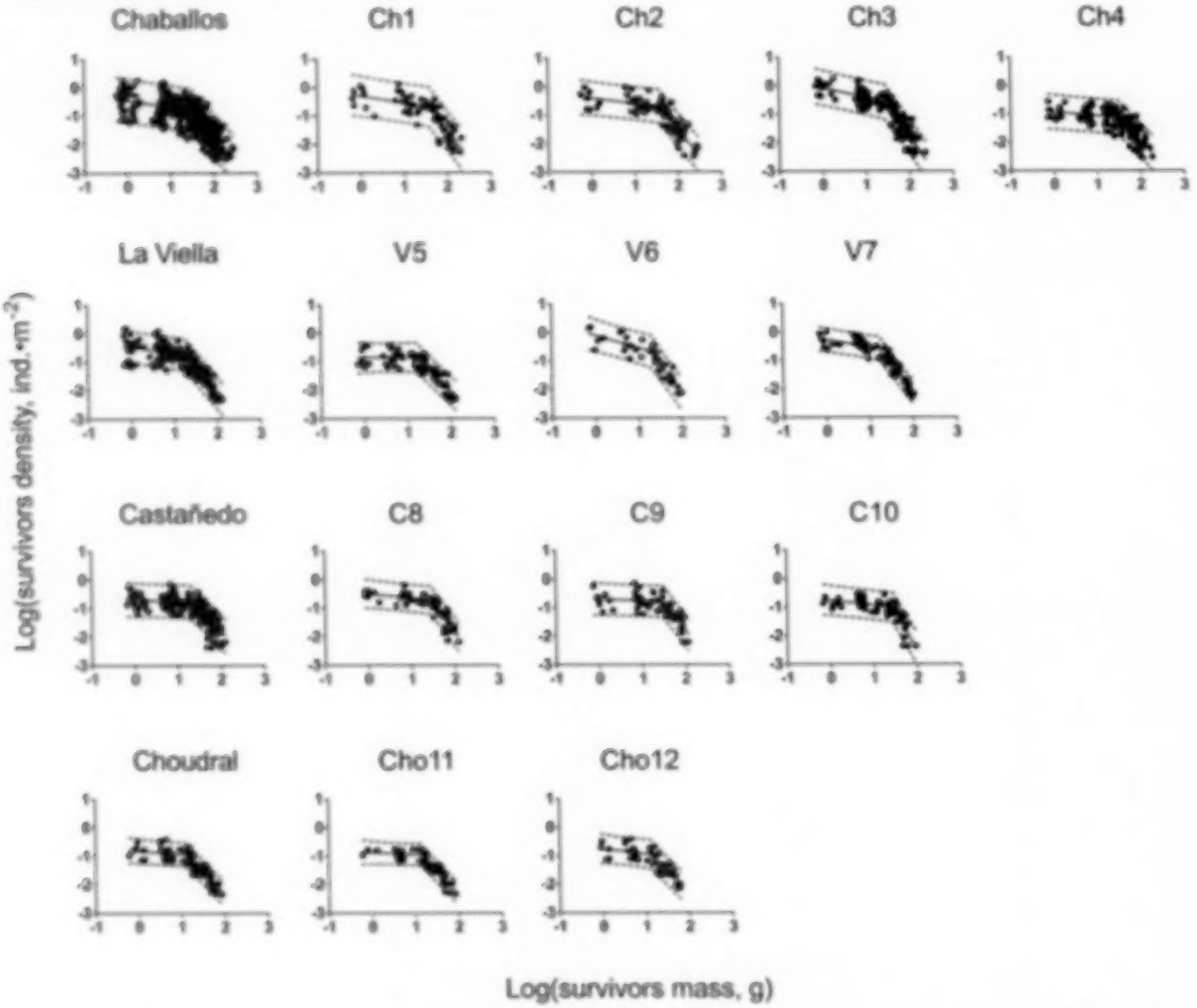
Fig. 2. Variations in log-transformed survivors density (individuals (ind.)·m^{-2}) over mass (grams) from recruitment to the complete disappearance of 110 cohorts of brown trout (*Salmo trutta*) at 12 study sites of Rio Chaballos (Ch1–Ch4), La Viella (V5–V7), Castañedo (C8–C10), and Choudral (Cho1–Cho2) (Rio Esva drainage, northwestern Spain). Fits of two-phase regressions (and 95% CI) for each single site (pooled cohorts) and streams (pooled sites and cohorts) are shown. The numbers of cohorts examined and other related information are presented in Table 1.



the first phase at sites of higher recruitment. Given low mortality during that first phase, the elevations (A_1) were also significantly correlated to the threshold densities (D_K) upon which the trajectories changed slope ($r^2 = 0.56$, $p = 0.01$).

In contrast, the threshold masses upon which the trajectories changed slope (K) appeared independent of the elevations (A_1; $r^2 = 0.16$, $p = 0.24$), of the slopes of the first phase (B_1; $r^2 = 0.09$, $p = 0.38$), and of the corresponding threshold densities (D_K; $r^2 = 0.008$, $p = 0.80$) and also were unrelated to the slopes of the second phase (B_2; $r^2 = 0.23$, $p = 0.16$). In turn, the threshold densities upon which the trajectories changed slope (D_K) were significantly related to the slopes of the second phase (B_2; $r^2 = 0.44$, $p = 0.036$), with steeper slopes at sites containing numerically stronger cohorts (Fig. 3*a*); these slopes of the second phase (B_2) were also related to the mean mass of individuals (W_s, g·individual^{-1}, a proxy of the growth experienced during the second phase; Fig. 3*b*). As a consequence, no intrinsic factor appeared to be related to the threshold masses, and these masses had no obvious effect on the slopes of the second phase. However, steeper slopes during the second phase occurred at sites of numerically stronger cohorts (i.e., D_K) and faster growth (i.e., W_s).

Density–mass coefficients in relation to extrinsic factors

The trajectories depicted by the coefficients of the two-phase relationships as a function of site depth revealed strongly consistent spatial patterns. The elevations (A_1; Fig. 4*a*), threshold densities (D_K; Fig. 4*b*), and slopes of the second phase (B_2; Fig. 4*d*) described parabolic curves as a

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Table 1. Coefficients (95% confidence interval, CI, in parentheses) of the two-phase regressions fitted to the log-transformed survivors density (individuals (ind.)·m^{-2}) against mass (grams) of brown trout (*Salmo trutta*) at the 12 study sites depicted in Fig. 2 of Chaballos (Ch1–Ch4), La Viella (V5–V8), Castañedo (C8–C10), and Choudral (Cho11–Cho12) and for single streams (pooled sites) and for the whole data set (streams and sites pooled).

Site	YC	N	Rc	A_1	B_1	K	B_2	r^2	K_x	D_x	M_x
Ch1	11	94	0.01–0.94	–0.31 (–0.54, –0.08)	–0.24 (–0.46, –0.01)	1.57 (1.39, 1.76)	–1.99* (–2.60, –1.37)	71.9	37.2	0.14	5.03
Ch2	10	87	0.07–0.95	–0.41 (–0.58, –0.24)	–0.18 (–0.35, –0.01)	1.56 (1.42, 1.69)	–1.86* (–2.21, –1.52)	78.1	36.1	0.20	7.33
Ch3	13	116	0.01–1.82	–0.07 (–0.23, 0.09)	–0.36* (–0.53, –0.17)	1.44 (1.32, 1.55)	–2.15* (–2.49, –1.80)	82.1	27.9	0.26	7.34
Ch4	13	128	0.01–0.25	–0.94 (–1.09, –0.79)	–0.12 (–0.28, 0.03)	1.48 (1.35, 1.61)	–1.56* (–1.98, –1.18)	60.8	30.2	0.06	1.74
Chaballos	47	425	0.01–1.82	–0.45 (–0.56, –0.34)	–0.24* (–0.36, –0.13)	1.45 (1.35, 1.56)	–1.64* (–1.89, –1.40)	61.8	28.2	0.14	3.94
V5	9	83	0.03–0.37	–0.88 (–1.02, –0.70)	–0.01 (–0.22, 0.23)	1.12 (1.06, 1.35)	–1.50* (–1.79, 1.20)	75.6	16.2	0.12	1.93
V6	9	80	0.07–1.43	–0.49 (–0.62, 0.23)	–0.44* (–0.75, –0.14)	1.29 (1.10, 1.49)	–2.16* (–2.70, –1.62)	87.0	19.5	0.19	3.71
V7	9	69	0.06–0.50	–0.29 (–0.42, –0.15)	–0.24 (–0.43, –0.05)	1.22 (1.10, 1.33)	–1.99* (–2.30, –1.68)	89.6	16.6	0.22	3.72
La Viella	27	232	0.03–1.82	–0.47 (–0.58, –0.35)	–0.21 (–0.37, –0.06)	1.25 (1.15, 1.35)	–1.82* (–2.06, –1.58)	77.8	17.8	0.18	3.20
C8	7	58	0.05–0.51	–0.49 (–0.68, –0.31)	–0.15 (–0.35, 0.05)	1.44 (1.32, 1.56)	–2.03* (–2.55, –1.52)	76.9	27.5	0.20	5.50
C9	8	65	0.06–0.56	–0.70 (–0.89, –0.51)	–0.06 (–0.26, 0.14)	1.47 (1.34, 1.60)	–1.98* (–2.56, –1.40)	66.9	29.6	0.16	4.86
C10	7	58	0.03–0.23	–0.82 (–0.93, –0.69)	–0.03 (–0.06, 0.01)	1.25 (1.32, 1.54)	–1.86* (–2.14, –1.69)	70.7	26.3	0.09	2.26
Castañedo	22	181	0.03–0.56	–0.67 (–0.82, –0.57)	–0.04 (–0.19, 0.11)	1.29 (1.18, 1.40)	–1.50* (–1.80, –1.21)	60.4	19.5	0.18	3.51
Cho11	6	72	0.07–0.17	–0.88 (–1.05, –0.70)	–0.07 (–0.32, 0.18)	1.13 (0.10, 1.26)	–1.60* (–1.90, –1.30)	85.6	13.2	0.11	1.45
Cho12	8	66	0.04–0.33	–0.75 (–0.96, –0.54)	–0.18 (–0.51, 0.15)	1.09 (0.89, 1.29)	–1.54* (–1.98, –1.10)	76.4	12.4	0.13	1.59
Choudral	14	138	0.04–0.33	–0.81 (–0.94, –0.68)	–0.13 (–0.33, 0.07)	1.11 (0.99, 1.22)	–1.56* (–1.81, –1.32)	81.3	12.9	0.09	1.16
Total	110	976	0.01–1.82	–0.56 (–0.63, –0.49)	–0.15 (–0.25, –0.05)	1.18 (1.10, 1.27)	–1.27* (–1.38, –1.15)	58.7	15.1	0.17	2.57

Note: YC, the number of cohorts analyzed; N, the number of data pairs; Rc, the range of recruitment (individuals·m^{-2}). Coefficients of the two-phase regressions for each site: A_1, the elevations; B_1 and B_2, the slopes of the first and second phases; K, the threshold mass; r^2, the variance explained. K_x is the threshold mass (grams), and D_x and M_x are the corresponding threshold density (individuals·m^{-2}) and threshold biomass (g·m^{-2}) at K, when the regression switched slope. All two-phase regressions are significant in $p < 0.001$; instances in which either the first or the second slope were significant are indicated with an asterisk (*).

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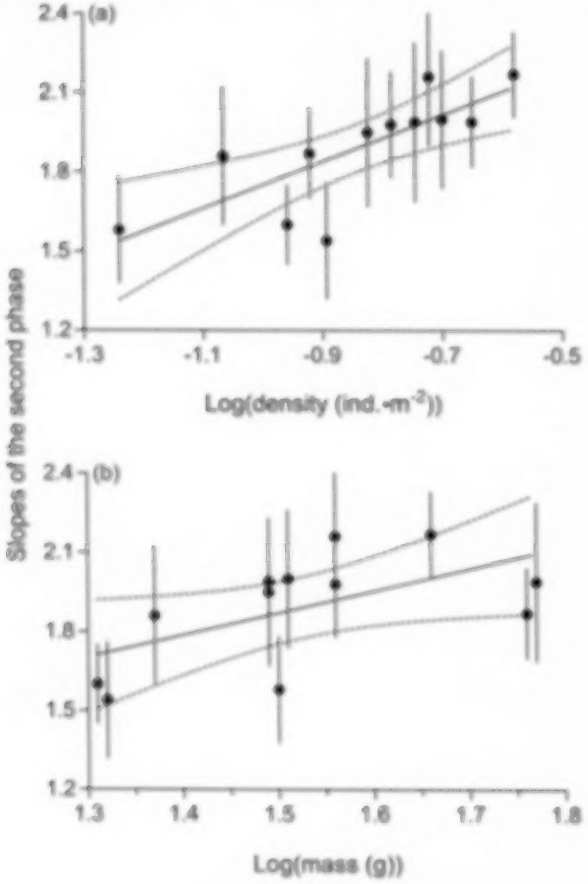
Fig. 3. Positive linear trends depicted by the slopes of the second phase (B_2, signed changed) in the density–mass relationships of brown trout (*Salmo trutta*) at 12 study sites against (*a*) log-transformed threshold densities (D_K, individuals (ind.)·m^{-2}). The linear regression (coefficients ± 1 standard error, SE, and significant level) is $B_2 = -2.635(\pm 0.11) - 0.088(\pm 0.22)D_K$; $r^2 = 0.60$, $p = 0.003$. (*b*) Log-transformed mass (W_K, g) during the second phase. The linear regression is $B_2 = -0.621(\pm 0.035) - 0.833(\pm 0.359)W_K$; $r^2 = 0.35$, $p = 0.04$.



function of site depth in which the three coefficients initially increased with increased site depth, peaked at sites of intermediate depth, and declined at the deeper sites. In contrast, the threshold masses (K) at which the slope changed direction increased linearly with increased site depth (Fig. 4*c*). These patterns are strongly consistent with the previously observed lack of significant correlation between the threshold masses and all other coefficients but significant correlations between the elevations, threshold densities, and slopes of the second phase.

Discussion

This study, based on the long-term monitoring of 110 cohorts of resident brown trout across sites and streams, highlighted robust relationships between density and mass across the lifetime of this salmonid. At all sites, density exhibited a nonlinear, two-phase trajectory with increased mass. During a prolonged time period, density changed little until a threshold mass was attained, after which density declined sharply with increasing mass until the complete disappearance of the cohorts. These patterns, with two phases of markedly different slopes, were consistent across cohorts, sites, and streams and matched the patterns elucidated in a recent comparison among three geographically disjunct populations of resident, lake-dwelling, and sea-migratory brown trout (Lobón-Cerviá and Mortensen 2006).

Within the stream sections included in this study, both structural features of the sites and population traits showed a strong tendency to be site-specific, as did the coefficients of the density–mass relationships. Recruitment, represented by the elevation of the density–mass relationships, varied substantially among sites and exhibited a parabolic trajectory as a function of site depth. In these relationships, recruitment was maximized at sites of intermediate depth and declined towards the opposing extremes to attain similarly low magnitudes in the shallowest and deepest sites. Beyond recruitment, no spatial or food-related factors appeared to limit density during a prolonged time period of intensive growth lasting for about half of the lifetime. During this first phase, the slopes of the density–mass relationships did not differ from zero, and in the few instances when these slopes were significant, the magnitudes attained were markedly below those predicted by the space or food demands; this pattern indicates that the cohorts were far below the carrying capacity of the sites.

This prethinning period ended when the individuals attained a threshold mass that varied among sites to an extent that the onset of higher mortality differed by about 1 year among sites. During the second phase, all slopes of the density–mass relationships were highly significant, varied widely among sites, and were substantially greater than those predicted by the food or space demands. Two intrinsic population factors, threshold density at the onset of the second phase, as a proxy of cohort strength, and mass, as a proxy of the growth experienced by individuals during the second phase, had strong effects on these slopes. This indicates that mortality increased at a greater rate at sites where more abundant individuals grew faster, which is strongly consistent with the major assumption of self-thinning that intensity of intraspecific competition determines how quickly the cohorts decline.

Previous studies on these populations revealed that the annual magnitude of recruitment across sites is determined by space availability during the emergence period. Space availability is in turn determined by the discharge conditions, whereas at a site scale, the annual magnitudes of recruitment are determined by interactions between discharge and stream channel structure (Lobón-Cerviá and Rincón 2004; Lobón-Cerviá 2007). Moreover, Rincón and Lobón-Cerviá (2002) argued that every stream section contains a specific amount of space suitable for individuals of a given size, with a scarcity of deeper waters suitable for larger individuals. As a consequence, growing individuals find increasingly fewer adequate foraging locations, resulting in greater mortality. Steingrímsson and Grant (1999) offered strong support for this hypothesis in a detailed study on Atlantic salmon (*Salmo salar*) in the Catamaran River (Canada), where shal-

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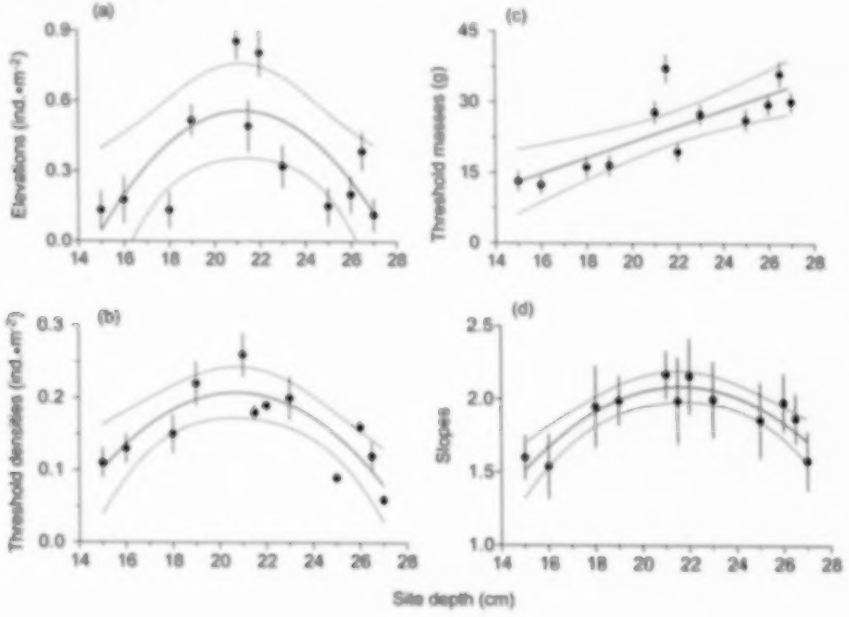
Fig. 4. Relationships depicted by the major coefficients of the two-phase density–mass relationships of brown trout (*Salmo trutta*) at 12 study sites against the mean depth of the sites (site depth, cm). (*a*) Concave trajectory described by the elevations (A_1, individuals (ind.)·m^{-2}, ± 1 standard error, SE). The quadratic function (coefficients ± 1 SE and significant level) is $A = -5.377(\pm2.14) + 0.559(\pm0.21)$Depth $- 0.013(\pm0.005)$Depth^2; $r^2 = 0.51$, $p < 0.01$. (*b*) Concave trajectory described by the threshold densities (D_K, ind.·m^{-2}). The quadratic function is $D_K = -1.182(\pm0.334) + 0.134(\pm0.032)$Depth $- 0.003(\pm0.001)$Depth^2; $r^2 = 0.69$, $p < 0.01$. (*c*) Positive linear trajectory described by the threshold masses (K, g ± 1 SE). The linear regression is $K = -12.4(\pm4.19) + 1.70(\pm0.29)$Depth; $r^2 = 0.59$, $p < 0.01$. (*d*) Concave trajectory described by the slopes of the second phase (B_2, sign changed, ± 1 SE). The quadratic function is $B_2 = -4.013(\pm1.02) + 0.56(\pm0.10)$Depth $- 0.01(\pm0.002)$Depth^2; $r^2 = 0.79$, $p < 0.001$.



lower sites enhanced loss rates and steeper self-thinning gradients relative to deeper sites. On the other hand, among-site differences in growth are widely reported in stream salmonids (Mann et al. 1989; Newman and Waters 1989). Differences in growth among nearby sites or streams subject to a common temperature regime have been attributed to variations in diet and foraging strategies (Bridcut and Giller 1995) and reflect patchiness in the production of food (Power 1973). It is, therefore, not surprising that in the present study, site depth had no obvious effects on growth but critical effects on density.

Consequently, this study further corroborates the importance of space availability in determining the numerical dynamics of the cohorts, while at the same time offering a new interpretation of the role of space. Here, the importance of the combined effects of food and space availability across spatial scales, which are governed by two different processes, are clear and compelling. Food is determined by the production system, which then results in a patchily distributed food supply (Pringle et al. 1988) and, hence, in differential growth among sites. In contrast, space availability is imposed by the physical structure of the stream channel, which defines different levels of space suitability for individuals of different size. This results in a patchwork of sites across stream gradients characterized by combinations of space availability, different growth intensities, and variable densities. As a consequence, the process underlying self-thinning relies on the interactions between variable space, growth, and density to induce different competitive interactions at a site scale. These competitive interactions then result in variable self-thinning coefficients, the magnitudes of which reflect the ability of trout to grow and survive in response to competition for the space available at the very local scale of the stream site.

When Steingrímsson and Grant (1999) and Rincón and Lobón-Cerviá (2002) discussed the importance of space availability for self-thinning gradients, they did not consider among-site differences in growth, only variations in the physical structure of the sites. They suggested that steeper self-thinning coefficients should occur at shallower sites, and shallower coefficients at deeper sites. Clearly, these patterns are consistent with the ascending phase of the parabolic curve defined in this study but not consistent with the descending phase. In the parabolic curve, the lowest coefficients occurred at the shallowest sites where trout also exhibited the lowest densities of slower growers. Greater growth and density probably increased competition, with highest competition intensity and steepest coefficients at sites of intermediate depth where both growth and density were maximized. Water depth acted as a proxy of sufficient space availability, where increasing water depth appears capable of weakening competition and reducing mortality at sites sufficiently voluminous, and therefore at these sites, the self-thinning coefficients declined with increased site depth.

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Thus, growth, density, and space availability interact with each other in a manner that offsets the predominant role of each factor.

In conclusion, when taken in combination with other studies (Lobón-Cerviá and Mortensen 2006), the results of this study offer empirical evidence of self-thinning as a common process in stream-living brown trout. These studies provide no evidence to support the occurrence of an invariant self-thinning coefficient (see also Nee et al. 2005). In contrast, patterns of different slopes in two phases with far more variation than previously reported by both empirical (Grant 1993, Elliott 1993, Bohlin et al. 1994) and experimental (Steingrímsson and Grant 1999; Keeley 2003) studies appear the rule rather than the exception.

In addition to the role of habitat quality elucidated in this study, other factors both intrinsic and extrinsic to the population may operate to inflate the self-thinning coefficients. For example, Dunham and Vinyard (1997) examined whole-population processes across temporal scales and revealed patterns similar to those for single cohorts; their results emphasize the importance of intercohort interactions. Moreover, unusual natural events such as droughts have also been reported to influence the self-thinning coefficients in brown trout (Elliott 1993) and other salmonids (Dunham and Vinyard 1997). Salmonids exhibit a variety in life history tactics in environmentally complex streams across climatic regions; numerous factors may operate on growth (Lobón-Cerviá 2005) and mortality (Hutchings 1993), and even metabolic rates may be mediated by temperature regimes (Clarke 2006). As a consequence, across their distributional range, we might expect to observe density–mass relationships with even greater variation than that reported in this study, including the variety of patterns reported in the literature (see Introduction). Although the self-thinning concept appears robust for stream-living salmonids, the variability exhibited by salmonids across streams suggests that applying a single self-thinning rule to the management of these populations (i.e., Armstrong 2005) appears premature and may not be straightforward.

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Intralacustrine site fidelity and nonrandom mating in the littoral-spawning northern redbelly dace (*Phoxinus eos*)

Rachel Massicotte, Pierre Magnan, and Bernard Angers

Abstract: Natal site fidelity of the northern redbelly dace (*Phoxinus eos*), a common minnow in North America, was confirmed by combining ecological and genetic approaches. A 2-year mark–recapture experiment conducted at four sites separated by 50–450 m strongly supported the propensity of the dace to practice site fidelity during the reproductive period. Individuals recaptured at their marking sites were characterized with five microsatellite loci. Hardy–Weinberg equilibrium and allelic differentiation tests revealed that the fish from different sites significantly differed from a single panmictic and genetically uniform population, thus confirming the homing behaviour of the dace. The detection of a pattern of isolation by distance revealed that migration mostly occurred between nearby sites and decreased as distance from birth site increased. When considering the high population density of dace, their high swimming capability, the distribution of the spawning sites along the littoral zone, and the small size of the lake studied (<5 ha), these results strongly suggest natal site fidelity in this species. The detection of this phenomenon for this species is extremely useful for empirical investigations of factors affecting patterns of isolation by distance and of evolutionary perspectives of natal site fidelity in fishes.

Résumé : Un comportement de fidélité au site de naissance du ventre rouge du nord (*Phoxinus eos*), un cyprin commun d'Amérique du Nord, a été confirmé par la combinaison d'approches écologique et génétique. Une expérience de marquage et recaptures répétées pendant 2 années sur quatre sites distants de 50 à 450 m supporte fortement la propension du cyprin au comportement de fidélité au site en période de reproduction. Les individus recapturés à leur site de marquage ont ensuite été caractérisés avec cinq microsatellites. Les tests d'équilibre de Hardy–Weinberg et de différenciation allélique révèlent que les poissons des différents sites diffèrent significativement d'une population panmictique et génétiquement uniforme, ce qui confirme le comportement de fidélité au site de naissance du cyprin. La détection d'un patron d'isolement par la distance révèle que les échanges de migrants sont plus importants entre des sites rapprochés et diminue avec une augmentation de la distance entre les sites de naissance et de ponte. En considérant la forte densité de cette population de cyprins, leur importante capacité natatoire, la distribution des sites de ponte le long de la zone littorale et la petite taille du lac étudié(<5 ha), ces résultats indiquent fortement l'existence d'un comportement de fidélité au site de naissance chez cette espèce. La détection de ce phénomène chez cette espèce la rend extrêmement utile pour l'étude empirique des facteurs qui affectent le patron d'isolement par la distance et des perspectives évolutives de la fidélité au site de naissance chez les poissons.

Introduction

Natural populations are generally genetically structured, with a higher frequency of mating between individuals that are geographically close and (or) that reproduce during the same period. Spatially or temporally structured populations will display different evolutionary properties and trajectories than will a randomly mating population (Hendry and Day 2005). Determining how individuals of a species are organized within a given habitat is a key feature in ecology (e.g., Excoffier 2001) and population management (e.g., Nielsen 1998). The analysis of genetic structure can also reveal evolutionary processes acting on populations.

While physical barriers and habitat discontinuities limit displacements, population structuring may also occur in a continuous habitat; each group of reproducing individuals may be panmictic within the group but isolated to some extent from other groups. In such a case, genetic differentiation can be modeled with Wright's (1943) isolation-by-distance (IBD) model, which predicts a positive correlation between genetic differentiation and geographical distance. The correlation between the geographic locations

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of parents and their offspring is generally related to the species' dispersal properties. Species with limited dispersal capabilities generally display a high level of population structure (e.g., Barluenga and Meyer 2005). Though a species with a high dispersal capability often evolves as a panmictic population (e.g., Teterina et al. 2005; Barluenga et al. 2006), it may display low variance in distance between birth and breeding sites owing to behaviours such as natal site fidelity. Natal site fidelity is characterized by the return and the reproduction of an individual to the site of its birth (Blair and Quinn 1989). For example, anadromous fish usually show high site fidelity for reproduction (Nielsen et al. 1999; Waters et al. 2000; King et al. 2001), which is referred to as philopatry or homing behaviour. When repeated over several generations, natal site fidelity restricts gene flow and allows progressive genetic differentiation and population structuring among spawning populations, even in the absence of geographic barriers (Leider et al. 1984; Varnavskaya et al. 1994; Hendry et al. 1995).

The northern redbelly dace (*Phoxinus eos*) is a small cyprinid fish widely distributed in lakes and streams of North America (Scott and Crossman 1973). Despite its small size (average 51 mm), this species is known to have a good swimming capacity (Trudel and Boisclair 1996) and performs daily migrations between the littoral and pelagic zones of lakes (Naud and Magnan 1988; Gauthier and Boisclair 1997). While the species has the capacity to disperse throughout a lake, individuals do not display a random distribution in the littoral zone and are frequently recaptured at the same locations (Magnin et al. 1976), suggesting that this species exhibits site fidelity behaviour to some extent. However, site fidelity alone is not expected to affect genetic structure unless fish reproduce at their birth site. In lakes, spawning takes place in masses of filamentous algae along the littoral zone (Cooper 1935). Such spawning habitats are likely more abundant and continuous than spawning habitats in tributary streams, which tend to be more discrete and fragmented in distribution (Dynes et al. 1999; Strange and Stepien 2007). Genetic structure in such a species with high dispersal capability and neighbouring spawning sites would then be interpreted as a strong correlation between birth and breeding sites.

The objective of this study was to confirm site fidelity and indirectly assess reproduction at the birth site in a littoral-spawning *P. eos* population. We used ecological observations (mark–recapture (MR)) made on four sites of a lake during the reproductive period combined with genetic analyses on individuals recaptured at their site (DNA polymorphism) to address this objective. The rational of the experiment is that a correlation between reproduction and birth sites is expected if individuals exhibit natal site fidelity. In such a case, individuals recaptured at a given site are expected to originate and reproduce at that site. If so, population genetics predict that pooling individuals from different mating sites will result in a deviation from Hardy–Weinberg equilibrium (HWE) while individuals from a given site are expected to reproduce panmictically. Secondly, in absence of barriers, individuals may reproduce at a site different from their birth place, but the number of migrants is then expected to decrease as the geographic distance between sites increases, resulting in an IBD pattern. In the absence of natal site fidelity, individuals are expected to be randomly distributed with respect to their birth site. In such a situation, recaptures are not expected to originate at that site and will represent a single panmictic population. As a result, no deviation from HWE, no genetic differentiation, and no IBD will be observed.

Materials and methods

MR experiment

The experiment was conducted in Lake Desjardins, southern Quebec, Canada (45°54′56.1″N, 74°04′26.3″W). This lake is 4.87 ha in surface area and has a perimeter of approximately 1791 m, a mean depth of 2 m, and a maximum depth of 8 m.

To investigate site fidelity during the reproductive period, an MR experiment was performed at four distinct sites (A, B, C, D) separated by 60–400 m to examine the influence of distance on migration (Fig. 1). Four unbaited commercial minnow traps per site, separated from each other by less than 4 m, were set between 0.5 and 1.5 m of depth in the littoral zone for 1 h. The experiment was performed at the end of the spring, which corresponds to the breeding period of *Phoxinus* (Scott and Crossman 1973). According to external characteristics (Scott and Crossman 1973), most individuals observed during the experiment were sexually mature. Females had to be handled with care, since the eggs of many were easily extruded, indicating that they were ready to spawn. Similarly, most of the males had thick pectoral fins; this trait is usually an indication of mating activity, though it remains for some time after mating.

Five marking sessions were performed at each of the four sites from 27 May to 10 June 2004 (Table 1). Approximately the same number of individuals was marked at the different sites, for a total of 7115 (Table 1). Fish from each of the four sites and five marking sessions were marked in a distinctive manner with a fluorescent elastomer using an elastomer tag air-driven injection system (Northwest Marine Technology). Prior to the experiment, we assessed how this tagging method affected *P. eos* survival by keeping 50 tagged and 50 untagged individuals under observation for 3 weeks in aquaria; no mortalities occurred in either group. To confirm that site fidelity is the result of the active return of individuals to their site of capture rather than restricted displacement (e.g., Gerking 1959), fish were released 20–30 m away from their capture site after a brief period of recovery (approximately 1 h). Six recapture sessions were performed in 2004 (28–29 May; 31 May – 1 June; 2–3, 9–10, 11, 15 June). An additional sampling session was performed 1 year later (9 June 2005) to assess site fidelity over a longer period. Each fish caught was examined for the presence of the fluorescent tag. Recaptured individuals were remarked according to the site and day of sampling (during the marking sessions only), allowing us to reconstruct the complete capture history for each individual.

A multistate Cormack–Jolly–Seber (CJS) analysis was performed to estimate the movements among sites, the survival rate (the probability of the animal surviving and remaining in the sample area), and the recapture probabilities for each site. The multistate CJS model for open populations is a generalization of the CJS model (Cormack 1964; Jolly

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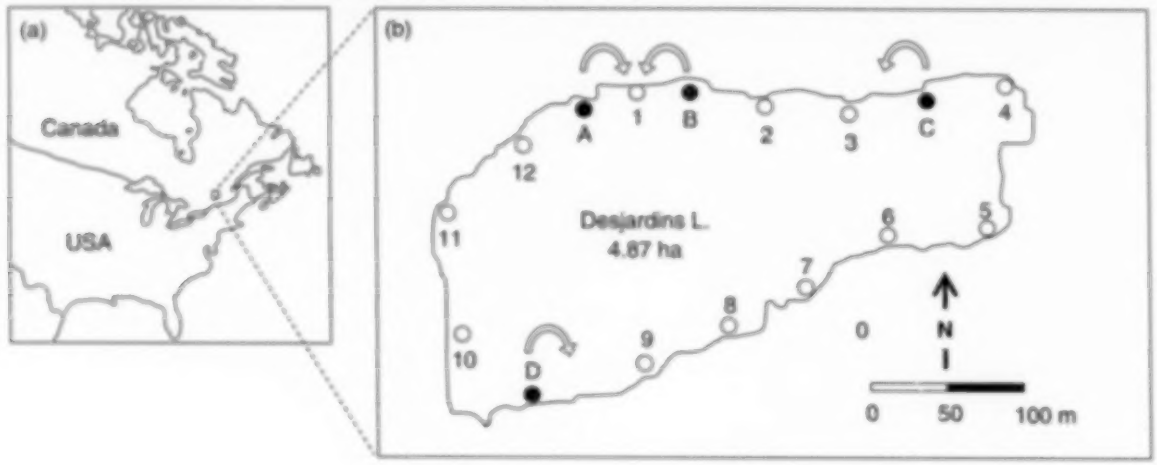
Fig. 1. Location of the study site: (*a*) map of northeastern North America; (*b*) map of Lake Desjardins. Solid circles (A, B, C, D) correspond to marking sites; open circles (1 to 12) represent the additional capture sites; arrows indicate release sites of marked individuals.



(45° 54' 56.1" N, 74° 04' 26.3" W)

Table 1. Number of individuals marked at the four study sites for each of the five marking sessions.

	Marking site			
Date	A	B	C	D
27 May	350	169	115	162
28–29 May	300	300	577	271
31 May – 1 June	497	429	492	212
2–3 June	315	272	157	655
9–10 June	295	547	500	500
Total	1757	1717	1841	1800

1965; Seber 1965) that allows transitions among states (e.g., that individuals of a population can be distributed across multiples sites; Williams et al. 2002). We used the Markovian model to estimate the movement and the survival probabilities independently. Three models that differ in the number of parameters estimated were tested: model D computes estimates under the assumption that survival–transition probabilities and capture probabilities are constant over time, model B assumes that survival–transition probabilities are constant over time but that capture probabilities are time-dependent, and model A assumes both survival–transition and capture probabilities are time dependent. The model with the lowest AIC_c value (Akaike's information criterion corrected for small sample sizes; Burnham and Anderson 2002) was considered the most appropriate model. The analysis was performed using the MSSURVIV program (Hines 1994).

To test the hypothesis of random distribution of marked individuals, χ^2 tests were performed. Because the number of marked individuals varied among sites (especially at the beginning of the MR experiment), the expected numbers of recaptures per site for a given session were adjusted according to the proportion of marked individuals (Table 2).

Because individuals that were not recaptured might have left their initial marking site but remained close by (restricted-movement paradigm: Rodriguez 2002), extensive sampling was performed to detect fish movements outside of the marking sites and to assess the distribution of migrants along the littoral zone. Twelve additional sites located between the marking sites (Fig. 1) were sampled following the same procedure outlined above on two different dates, 2–3 and 17–18 June 2004. Each fish caught was examined for the presence of marks and released at its site of capture. These direct observations of the number of migrants were used to assess IBD (see below).

Genetic analyses

We characterized the population of a given site by assuming that individuals recaptured at their marking site during the reproductive period reproduce at that site. A small piece of the caudal fin of recaptured individuals was taken and preserved in 95% ethanol. Total DNA was extracted from that piece of tissue by proteinase K digestion followed by phenol–chloroform purification and ethanol precipitation (Sambrook et al. 1989).

Because this lake is known to contain both *P. eos* and hybrids (*P. eos-neogaeus*) (Angers and Schlosser 2007), the proportion of each form was determined from a subsample of 266 individuals randomly selected across recapture dates. Individuals were identified using genetic markers according to Binet and Angers (2005). Briefly, hybrids are perpetuated clonally (Goddard et al. 1998) and are thus characterized by the presence of one set of chromosomes from *P. eos* and one set from *P. neogaeus*. To determine the nuclear genomic composition of an individual, an intron of the growth hormone gene and one of the mesoderm specific transcript gene were amplified by polymerase chain reaction (PCR). Primers of each locus are designed to provide PCR products of different sizes for *P. eos* and *P. neogaeus*, allowing chromosome identification. Individuals that displayed alleles of both sizes were classified as hybrids.

To assess the genetic signature of natal site fidelity, 24 to

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Table 2. Number of recaptures at the four marking sites.

Recapture site	Marking site A	B	C	D	Total
2004					
A	151 (20)	2	3	6	162 (2439)
B	8	150 (27)	8	5	171 (2724)
C	5	16	127 (21)	10	158 (3883)
D	8	8	3	104 (7)	123 (3282)
Total	172	176	141	125	614 (12328)
2005					
A	15	0	0	2	17 (736)
B	4	19	2	0	25 (848)
C	1	1	11	3	16 (737)
D	2	2	3	11	18 (752)
Total	22	22	16	16	76 (3073)

Note: The diagonal represents the number of individuals that were recaptured at their marking site. For marking site, multiple recaptures are given in parentheses; for total, numbers in parentheses refer to the total number of captures at the marking site.

44 recaptured individuals identified as *P. eos* were analyzed per site for a total of 139 individuals. These individuals were genotyped with five polymorphic microsatellite DNA loci markers developed for *P. eos*: *Pho-1* and *Pho-2* (Binet and Angers 2005) and *Pho-4*, *Pho-60*, and *Pho-61* (Angers and Schlosser 2007). PCR conditions and polymorphism detection were similar to those published in Binet and Angers (2005).

Genetic diversity was estimated with the total number of alleles (A), the allelic richness (A_R) using the rarefaction index proposed by El Mousadik and Petit (1996), and with Nei's (1987) measure of gene diversity (H_E) using the software FSTAT version 2.9.3 (Goudet 2001). The significance of differences in genetic diversity among the sites was tested using a paired t test on A, A_R, and H_E values at individual loci (Nei 1987). If natal site fidelity is occurring, individuals do not have the same probability of reproducing with each other, thus such a sample should deviate from Hardy–Weinberg expectations because of an excess of homozygotes (Raymond and Rousset 1995). On the other hand, individuals from a given site are expected to be drawn from a panmictic group that would fit with HWE predictions. This was tested by comparing the HWE of all sites taken together and each site independently using the probability test (HWE) and the global test across loci (homozygote excess) from the GENEPOP program version 3.4 (Raymond and Rousset 1995). The presence of null alleles that may generate homozygote excess and mimic the effect of nonrandom mating was assessed for each locus and site using the Micro-Checker package, version 2.2.3 (Van Oosterhout et al. 2003), and with the score test (U test) provided with the GENEPOP program (see Girard and Angers 2007).

To assess the consequence of natal site fidelity on genetic structure, allelic differentiation was tested over all sites with Fisher's exact test by means of a Markov chain Monte Carlo variation using the GENEPOP program (Raymond and Rousset 1995). Pairwise comparisons were also computed to identify the most different sites. F_{ST} estimator (Weir and Cockerham 1984) was measured and significance was assessed by permutation of individuals using the GENETIX program, version 4.05.2 (Belkhir et al. 2004).

IBD

A major expectation of the IBD model is that the number of migrants decreases as the distance between the birth and reproductive sites increases. This was tested using the MR results as well as the genetic data. The number of migrants detected during the MR experiment was reported as the sum of all individuals recaptured within each distance interval of 75 m from a marking site. The effective number of migrants exchanged per generation ($N_e m$) between each pair of sites was estimated with the private alleles method (Slatkin 1985; Barton and Slatkin 1986) using the GENEPOP program (Raymond and Rousset 1995). This estimation is recommended when the populations does not fit with an island model of migration or migration–drift equilibrium (Barton and Slatkin 1986). Distance between sites was measured along the littoral zone. The significance of the correlation between the number of migrants and the distance between sites was tested with the Pearson coefficient for MR results and with the Mantel test (Mantel 1967) for $N_e m$.

Results

MR experiment

A total of 614 recaptures were made at the four marking sites in 2004 (Table 2). Of these recaptures, 532 (86.6%) were caught at their original marking site in 2004 (Table 2). Furthermore, 63 individuals (11.8%) were captured at their marking site a third time and 12 (2.25%) a fourth time. Similarly, a high proportion of individuals (56 of the 76 recaptures, 74%) were again found on their marking site 1 year after the marking experiment (Table 2).

The model assuming that survival and movement probabilities are constant over time but that recapture probabilities are time dependent (model B) provided the lowest AIC_c value. The result of the multistate CJS analysis indicates that the survival probabilities were high and constant for

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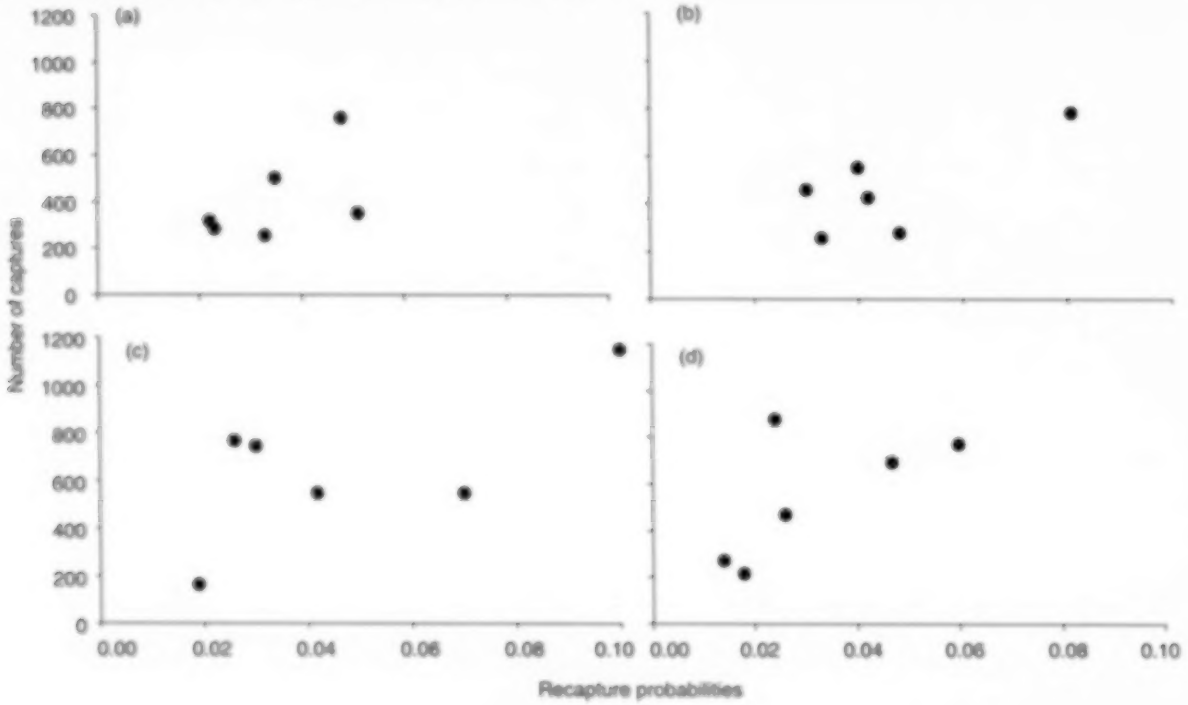
Fig. 2. Relationships between the recapture probabilities (multistate Cormack–Jolly–Seber analysis) and the total number of captures for each marking site (A, B, C, D) during the six recapture sessions in 2004.



each site (A: 0.93, B: 0.98, C: 0.76, D: 0.87). These high probabilities indicate that individuals have a high probability of surviving and remaining at their marking site. However, the estimated recapture probabilities are very low (mean ± standard deviation (SD) = 0.04 ± 0.02), indicating that if an individual was alive and present at a given site, it has a low probability of being recaptured. According to the model selected, recapture probabilities are time dependent, ranging from 0.014 to 0.1, but appear to be related to the success of capture (Fig. 2). In a closed population, recapture probabilities depend on both population size and the number of individuals caught (Davidson and Armstrong 2002).

The result of the multistate CJS analysis indicates that movement probabilities among sites (the probability of an individual to migrate to another site) are very low (Table 3). For example, the probability that an individual marked at site A would move to sites B, C, or D is 0.021, 0.010, and 0.023, respectively. The χ^2 tests used to test for a random distribution of individuals were highly significant for each site and each sampling day in 2004 and 2005 ($P < 0.001$), except for two sites on the first date of recapture (χ^2_1, site C: $P = 0.216$; site D: $P = 0.04$).

HWE and differentiation

The microsatellite loci were extremely variable and exhibited between 6 and 17 alleles in the 139 individuals recaptured at their marking site (Table 4; Fig. 3). A per site varied from 43 to 48 (Table 5). The difference between the mean A per site (45) and the total A (60) was not observed on either A_R (41.1 vs. 41.2, Table 5) or H_E (0.7824 vs. 0.7843, Table 5). No significant difference among sites was detected for A ($P > 0.326$), A_R ($P > 0.465$), or H_E ($P > 0.391$). These results indicate heterogeneous distribution of alleles (especially rare alleles that have a minor influence on H_E), but similar levels of diversity among sites.

When all individuals recaptured were considered as a single population, a significant departure from HWE (probability test over all loci: $P = 0.0364$) and a homozygote excess (global test: $P = 0.0163$) were observed (Table 5). This indicates that individuals sampled throughout the lake did not represent a panmictic population. When tested individually, two loci (*Pho-2*, $P = 0.0481$; and *Pho-1*, $P = 0.0650$) displayed significant or nearly significant departure, indicating that significant departure over all loci was not the result of a single marker. On the other hand, individuals recaptured at their marking sites appear to reproduce as a panmictic unit, as no departure from HWE was detected (Table 5). The tests failed to detect null alleles within sites at any of the loci analyzed.

The global test of allelic differentiation is significant ($P = 0.0256$). This suggests that the sites, or at least some of them, represent distinct reproductive units with restricted gene flow between them. Over all loci, significant results of allelic differentiation were observed for two pairwise comparisons (A–C, $P = 0.0158$; A–D, $P = 0.0195$), but these results are no longer significant after sequential Bonferroni correction. These tests also revealed that all pairs of sites differed at least at one locus, and all loci were different for

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Table 3. Movement probabilities (± standard deviation, SD) between the four marking sites.

Marking site	Recapture site			
	A	B	C	D
A	0.946±0.01	0.021±0.007	0.01±0.005	0.023±0.009
B	0.0043±0.003	0.935±0.02	0.036±0.01	0.025±0.009
C	0.009±0.006	0.035±0.01	0.927±0.02	0.029±0.01
D	0.019±0.008	0.013±0.007	0.036±0.01	0.932±0.02

Table 4. Characteristics of genetic markers used in this study.

Locus	Diversity indices			Null allele tests	
	A	H_O	H_E	M-C	UT
Pho-1	15 (10.5±1.3)	0.8613 (0.8642±0.0637)	0.8426 (0.8404±0.0117)	No	≥0.1210
Pho-2	17 (13.8±2.1)	0.8582 (0.8574±0.0256)	0.8927 (0.8913±0.0128)	No	≥0.0868
Pho-4	6 (5.5±0.6)	0.6978 (0.6886±0.0522)	0.7326 (0.7285±0.0440)	No	≥0.0742
Pho-60	11 (8±0.8)	0.7742 (0.7873±0.0904)	0.7738 (0.7665±0.0384)	No	≥0.0819
Pho-61	11 (7.8±1.3)	0.6379 (0.6376±0.0332)	0.6800 (0.6853±0.0586)	No	≥0.1564

Note: For each locus, data is given for the number of alleles (*A*), observed heterozygosity (H_O), Nei's gene diversity (H_E) over all sites (mean ± standard deviation, SD). Results of the null allele tests performed on each site are also given (M-C, Micro-Checker; UT, *U* test).

at least one pair of sites. These results indicated a very low divergence among sites, but altogether, the sites did not represent a genetically uniform population. The F_{ST} estimate over all sites is consistent with this interpretation, being very low (0.00530) but significant after permutation of individuals ($P = 0.0458$).

Migration and IBD

The littoral sampling over the 16 sites (including the four marking sites) allowed the recapture of 129 and 238 individuals for the first and the second sampling sessions, respectively. Of these recaptures, 73 (56.6%) and 134 (56.3%) were caught at their marking site during the first and the second sampling sessions, respectively. When considering the number of captures per site, the proportion of faithful individuals (2–3 June: 73/1434 = 5.09%; 17–18 June: 134/1510 = 8.87%) was higher than the total number of migrants captured at the 15 other sites (2–3 June: 56/4853 = 1.15%; 17–18 June: 104/7027 = 1.48%). Chi-squared tests performed between faithful individuals and migrants are highly significant for both periods ($\chi^2 > 80$, $P > 0.00001$).

These results indicate that the migrants are not randomly distributed along the littoral zone. In addition, we observed a decrease in the number of migrants with an increase in the distance between marking and capture sites for both the MR results and the genetic data (Fig. 4). The correlation between the number of migrants (log) estimated by the MR experiment and the distance (log) between the marking site and the recapture site (excluding recaptures at marking sites) is high and significant for both dates (2–3 June 2004: $r = -0.856$, $P = 0.015$; 17–18 June 2004: $r = -0.986$, $P < 0.0001$). The number of migrants per generation (N_fm) estimated with the private alleles method varied from 4.5 to 9.5 between sites. The Mantel test between N_fm and distance between sites (Fig. 4) is also highly significant ($r = -0.951$, $P < 0.0001$).

Discussion

Site fidelity

The MR experiments confirmed previous observations (Magnin et al. 1976) that *P. eos* does not distribute randomly along the littoral zone but rather exhibits site fidelity. Most individuals were recaptured at their marking site, and several were recaptured three or four times at the same location. Given the low recapture probabilities, recapturing individuals several times at the same site indicates that there is a strong propensity for individuals to return to their site of capture. The very low movement probability among sites that was estimated by the multistate CJS analysis confirmed that there is a higher probability of recapturing an individual at its marking site than at any other sample site in the lake.

The results of this study also confirm that site fidelity is not the result of restricted displacement during the reproductive period (e.g., Gerking 1959; Hert 1992). Recaptures of the marked individuals in all sites along the littoral zone show that this cyprinid has a high displacement capacity (Trudel and Boisclair 1996). Nevertheless, most individuals were recaptured at their marking site even though they had been displaced by 20–30 m. For example, individuals marked at sites A and B (separated by 60 m) were released midway between the two sites. Individuals were mostly recaptured at their marking sites, while very few were recaptured at the release site. This indicates that fish left the release site and actively returned to their site of capture, showing evidence of site fidelity. In addition, the recapture of individuals at their marking sites 1 year after the marking session clearly indicates that *P. eos* shows natal site fidelity and possesses mechanisms allowing site recognition in the littoral zone. Even though these mechanisms have been extensively studied in salmonid species, they are poorly understood in other freshwater fish species (e.g., Werner and Lannoo 1994).

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Fig. 3. Allelic frequencies at the five microsatellite loci for the sampled sites. Each circle represents one allele and the size of the circle represents its frequency. The *y* axis indicates relative allele size. Letters correspond to sites from Lake Desjardins (A, B, C, D).

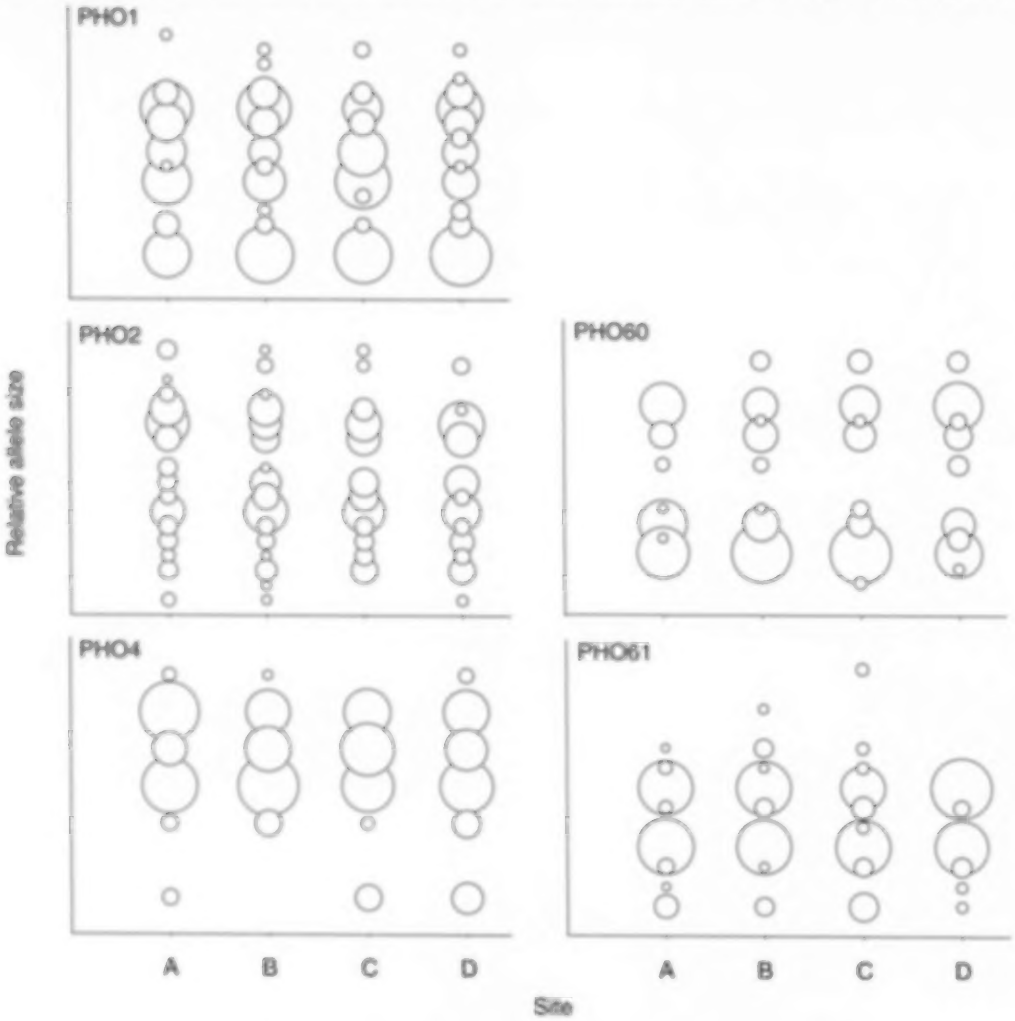

Table 5. Number of individuals analyzed (n), number of alleles (A) (allelic richness (A_R) in parentheses) estimated from 21 individuals, observed heterozygosity (H_O) and Nei's gene diversity (H_E) over all loci, and P value of Hardy–Weinberg equilibrium (HWE) probability test and global test across loci (homozygote excess).

Site	n	A (A_R)	H_O	H_E	HWE probability test	Homozygote excess
A	44	46 (39.6)	0.7689	0.7720	0.7591	0.1124
B	37	48 (41.3)	0.7439	0.7751	0.3854	0.3494
C	24	43 (41.9)	0.7917	0.7926	0.1395	0.4135
D	34	45 (41.5)	0.7636	0.7898	0.9297	0.0851
Total	139	60 (41.2)	0.7659	0.7843	0.0364*	0.0163*
Mean	34.8	45.5 (41.1)	0.7670	0.7824		

*$P < 0.05$.

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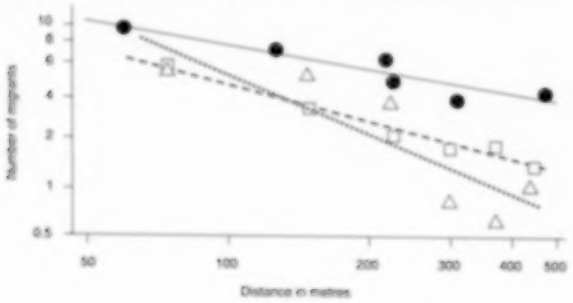
Fig. 4. Relationships between the number of migrants and the distance between marking and capture sites. Triangles and squares refer to recaptures made during the littoral sampling of 2–3 June and 17–18 June 2004, respectively. Solid circles refer to the number of migrants per generation ($N_e m$) estimated from genetic data.



The high survival probability (which includes the probability of individuals to be present at their site) indicates that the low recapture success is not the result of high mortality and (or) movement of individuals to other sites. Elastomer tags have been successfully used with many organisms, including fishes (Dewey and Zigler 1996; Frederic 1997), and we observed no mortality in either tagged or untagged fish after 3 weeks in aquaria. The low recapture success thus appears to be due to the high population density. Assuming each site to be a closed population, size estimates (number of captures divided by recapture probability; Davidson and Armstrong 2002) varied from 10 000 to 18 800 individuals per site. While these estimates must be considered with caution, they reveal the high population density in the littoral zone. The passive capture of an average of 87 to 139 individuals per trap per hour and the increase of recapture probability with the number of captures are consistent with the high population density hypothesis.

Natal site fidelity

Genetic analyses confirmed that the site fidelity observed in the littoral zone during the reproductive period of *P. eos* is more specifically natal site fidelity. While a direct assessment of natal site fidelity would have been to tag fish before they left their birth site and show that individuals spawn at the site they were born, genetic analyses provide an indirect assessment of natal site fidelity. The HWE tests clearly revealed that each local site (or at least some of them), and not the whole lake, is organized as a panmictic reproductive unit. Such results could occur only if individuals return to their birth site for reproduction. If individuals chose their spawning sites randomly, the entire population would have evolved as a single panmictic unit, even if these individuals subsequently returned to the same sites. These results are consistent with the numerous studies that report natal site fidelity in freshwater fish species (L'Abée-Lund and Vallestad 1985; Crossman 1990; Ridgway et al. 1991), though the phenomenon has rarely been confirmed with genetic analyses (Gross et al. 1994; Miller et al. 2001; Adams et al. 2006).

Given the scale of the study site, the presence of numerous spawning sites along the littoral area, and the high population density, differentiation among sampling sites, even if very small, reflects the natal site fidelity behaviour in this species. However, the fact that HWE over all individuals, allelic differentiation, and F_{ST} provide significant results revealed that gene flow among sites is not high enough to homogenize the genetic composition of sites (at least some of them). The very low levels of differentiation is a hallmark of recent intralacustrine populations of fish; F_{ST} values among populations that diverge since the end of Pleistocene ranging from 0.002 to 0.043 were observed for sockeye salmon (*Oncorhyncus nerka*) (Varnavskaya et al. 1994), while a value of 0.03 was reported for stone loach (*Barbatula barbatula*) of Lake Constance (Barluenga and Meyer 2005) and 0.029 was found for walleye (*Sander vitreus vitreus*) in the Great Lakes (Strange and Stepien 2007). Examples of large differentiation generally occur when multiple evolutionary groups coexist, such as the result of colonization from distinct glacial origins (e.g., Barluenga and Meyer 2005; Fraser and Bernatchez 2005). Intralacustrine populations are also generally characterized by scarce and discrete spawning sites (Dynes et al. 1999; Miller et al. 2001; Strange and Stepien 2007). The presence of a few discrete spawning zones may restrict gene flow among spawning sites, as the probability of straying is expected to be reduced in the absence of alternative spawning sites near the birth site.

The pattern of IBD detected from genetic polymorphism represents concrete evidence of the long-term organization resulting from natal site fidelity. Our results indicate that most of the individuals reproduce at their birth site and that migrants reproduce less frequently as the distance between the birth and breeding sites increases. The number of migrants estimated from genetic data are expected to differ from those based on the MR experiment; the former integrate over a long period the effects of migrants that are reproducing, while the latter represent a snapshot of the migration. Nevertheless, the slopes of both estimates are consistent with what would be expected if the number of migrants that reproduced successfully in the new habitat were proportional to the total number of migrants. The extensive recapture sessions conducted to detect fish movements outside of the marking sites confirmed that a substantial number of individuals moved along the littoral zone after being marked, but that their distribution was not random. Most individuals were recaptured close to their marking site, and their abundance decreased as the distance from the marking site increased.

In conclusion, this study reveals that in spite of a continuous distribution in the littoral zone and a high dispersal capability, fish may display a structured genetic organization at a very fine geographical scale. To our knowledge, the northern redbelly dace from Lake Desjardins shows an IBD pattern occurring at a much more restricted geographical scale than what has been previously observed. However, studies of IBD at a fine geographical scale are not common in temperate fish (Carlsson and Nilsson 2000; Barluenga and Meyer 2005). We believe that this species represents an excellent model for the study of the evolutionary perspectives of natal site fidelity and of the empirical factors characterizing IBD, such as population density (Gandon and Rousset 1999), distance between sites and barriers to dispersal (Taylor et al. 2003), and time since colonization (Crispo and Hendry 2005). Because the lakes inhabited by *P. eos* present very different characteristics, this species allows the investigation of many of these aspects.

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Additional features characteristic of this species make natal site fidelity of particular interest. First, this species displays a large variability in phenotypic characters (Schlosser et al. 1998). Natal site fidelity may then facilitate morphological differentiation and the formation of local adaptations within a given lake (Taylor 1991). Second, in the *Phoxinus eos-neogaeus* complex, the clonal hybrids are generally found in sympatry with *P. eos* (Angers and Schlosser 2007) and depend on their sperm for perpetuation (Goddard and Dawley 1990). While a sexual species is expected to have a larger ecological niche than asexual hybrids (Vrijenhoek 1994), natal site fidelity may reinforce the spatial isolation of a portion of the sexual species during the reproduction and prevent their extinction.

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The influence of hydrographic structure and seasonal run timing on genetic diversity and isolation-by-distance in chum salmon (*Oncorhynchus keta*)

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Abstract: We used 20 microsatellite loci to compare genetic diversity and patterns of isolation-by-distance among three groups of chum salmon (*Oncorhynchus keta*) from two physically distinct watersheds in western Alaska, USA. The results were consistent with the hypothesis that gene flow decreases as the complexity of the hydrographic system increases. Specifically, higher gene flow was inferred among 11 populations from a nonhierarchical collection of short coastal rivers in Norton Sound compared with 29 populations from a complex hierarchical network of inland tributaries of the Yukon River. Within the Yukon River, inferred gene flow was highest among 15 summer-run populations that spawn in the lower drainage, compared with 14 fall-run populations that spawn in the upper drainage. The results suggest that the complexity of the hydrographic system may influence population connectivity and hence the level of genetic diversity of western Alaska chum salmon. Finally, evidence of isolation-by-time, when controlling for geographic distance, supported the hypothesis that genetic divergence in Yukon River chum salmon is influenced by seasonal run timing. However, evidence of isolation-by-distance, when controlling for season run timing, indicated the populations are not sufficiently isolated, spatially or temporally, to prevent gene flow. Dispersal among summer- and fall-run populations may play a role in maintaining genetic diversity.

Résumé : L'analyse de 20 locus microsatellites nous a permis de comparer la diversité génétique et les patrons d'isolement par la distance chez trois groupes de saumons kéta (*Oncorhynchus keta*) de deux bassins versants physiquement distincts de l'ouest de l'Alaska, É.-U. Nos résultats s'accordent avec l'hypothèse selon laquelle le flux génique décroît lorsque la complexité du système hydrographique augmente. En particulier, nous avons déduit un flux génique plus important dans 11 populations dans un ensemble non hiérarchique de rivières côtières courtes dans le détroit de Norton par comparaison à 29 populations d'un réseau hiérarchique complexe de tributaires du fleuve Yukon à l'intérieur des terres. Dans le fleuve Yukon, le flux génique estimé est maximal chez 15 populations à montaison estivale qui fraient dans le bassin versant inférieur, par rapport à 14 populations à montaison automnale qui fraient dans le bassin versant supérieur. Nos résultats laissent croire que la complexité du système hydrographique peut influencer la connectivité des populations et donc le niveau de diversité génétique chez les saumons kéta de l'ouest de l'Alaska. Enfin, des indications d'un isolement par le temps, après correction pour la distance géographique, appuient l'hypothèse selon laquelle la divergence génétique chez les saumons kéta du fleuve Yukon est influencée par la saison de la montaison. Cependant, les indications d'isolement par la distance, après correction pour le moment de la montaison, indiquent que les populations ne sont pas suffisamment isolées dans l'espace et le temps pour empêcher le flux génique. La dispersion au sein des populations à montaisons estivale et automnale peut jouer un rôle dans le maintien de la diversité génétique.

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Introduction

Understanding how variation in habitat structure influences gene flow is important for developing sound management and conservation plans for exploited species (Frankham et al. 2002). This knowledge is particularly relevant for broadly distributed philopatric species like anadromous Pacific salmon (*Oncorhynchus* spp.) because the physical nature of the natal watershed (the hydrographic structure) can vary widely within and among species (Quinn 2005). Unfortunately, direct estimates of immigration rates for Pacific salmon are difficult to obtain, and few exist. Nevertheless, studies have indicated that the degree of genetic divergence among populations is generally inversely proportional to the degree of spatial isolation during spawning (Hendry et al. 2004). This trend of isolation-by-distance (IBD) (Wright 1931) indicates spatial separation alone can constrain the relative rate of gene flow. However, the extent to which variation in hydrographic structure influences IBD and, by inference, gene flow is not clear.

Ecological theory on the fitness costs and benefits associated with the alternative behaviors of philopatry (homing) and dispersal (gene flow or straying) provides a framework to hypothesize the influence of hydrographic structure on the IBD pattern in Pacific salmon (Hendry et al. 2004; Quinn 2005). For example, consider two hydrographically distinct watersheds: a nonhierarchical collection of short coastal rivers with temporally variable habitat quality and a single hierarchical river network of inland tributaries with high spatial habitat heterogeneity. Theory predicts that the more hydrographically complex river network will require more complex migration, promoting greater local adaptation, and conferring greater fitness benefit to philopatric individuals and higher fitness cost to immigrants (Hendry et al. 2004; Quinn 2005). In contrast, the less hydrographically complex collection of short coastal rivers will require less complex migration, conferring a lower fitness cost to immigrants especially if gene flow buffers against temporal variation in habitat quality. Based on these expectations, and assuming population size is known, we can predict measurable differences in the IBD model (e.g., Garant et al. 2000; Whiteley et al. 2004). For example, greater gene flow should result in lower variance in pairwise estimates of genetic divergence and a smaller slope of the linear regression of genetic divergence versus geographic distance (Slatkin 1993; Hutchison and Templeton 1999).

Chum salmon (*Oncorhynchus keta*) in northwest Alaska provide a good opportunity to test these predictions. The region includes two distinct but contiguous watersheds, Norton Sound and the Yukon River. The Norton Sound watershed ($\sim$50 000 km^2) is a collection of relatively short coastal rivers (mean length $\sim$110 km) distributed along $\sim$800 km of concave shoreline opening west to the Bering Sea (Brabets et al. 2000) (Fig. 1). The Yukon River watershed ($\sim$856 000 km^2) is a complex hierarchical network of inland tributaries traversing Alaska, with headwaters in British Columbia over 3000 km from the mouth (Fig. 1). Census data and escapement goals indicate Norton Sound populations are smaller than most Yukon River populations (Brannian et al. 2006) (Table 1).

Chum salmon in the Yukon River also exhibit a seasonal dichotomy in adult run timing that could influence gene flow. Summer-run populations typically enter the river in June and July and tend to spawn in downwelling areas in the lower and middle drainage. Fall-run populations typically enter the river in July and August and spawn in upwelling areas in the middle and upper drainage (Maclean 2003; Clark et al. 2006; Bue et al. 2006). Much of the genetic population structure in northwest Alaska chum salmon is explained by this seasonal (bimodal but overlapping) run timing (Wilmot et al. 1994; Seeb and Crane 1999). However, it is not clear if run timing impedes gene flow because the two groups are largely spatially distinct.

Here we test two hypotheses concerning the influence of hydrographic structure and seasonal run timing on gene flow among western Alaska chum salmon populations. First, we test the hypothesis that gene flow decreases as the complexity of the hydrographic system increases. We therefore predict that gene flow will be highest among Norton Sound populations, intermediate for Yukon River summer-run populations, and lowest for Yukon River fall-run populations. Gene flow is expected to be highest in Norton Sound because the hydrographic structure is not hierarchical (all rivers flow into the same marine area), and most populations spawn relatively close (<100 km) to saltwater. Gene flow is expected to be intermediate for Yukon River summer-run chum salmon because they reside in the lower to middle drainage, requiring a less complex migration than the fall-run populations, which spawn in upwelling areas in the middle and upper drainage. Second, we predict that genetic divergence in Yukon River chum salmon is influenced by seasonal run timing. Seasonal run timing has been shown to influence genetic divergence in Pacific salmon; however, in many instances the confounding influence of spatial isolation was not accounted for (Hendry and Day 2005). We address both hypotheses by evaluating intra- and interpopulation diversity and the IBD model.

Materials and methods

Sample collection and microsatellite genotyping

Fin tissue samples for DNA analysis were collected from adult chum salmon in 11 summer-run populations in Norton Sound and in 15 summer-run and 14 fall-run populations in the Yukon River (Fig. 1, Table 1). Sample sizes ranged from 40 to 100. Each individual sample was preserved in 95% ethanol in a 2 mL vial. Total genomic DNA was isolated from approximately 10–20 mg of fin tissue using a Promega Wizard SV 96 Genomic DNA Purification System. Each individual was genotyped using 20 microsatellite loci (Appendix A; Tables A1–A3). Genotyping details are described in Olsen et al. (2006).

Genetic diversity within populations

Estimates of allele frequency, allelic richness (A_r), and observed and expected heterozygosity (H_o, H_e) were computed for each locus and population sample using the computer program FSTAT version 2.9.3 (Goudet 2001). Estimates of allelic richness were computed according to El Mousadik and Petit (1996) using the rarefaction index. A randomization test of the statistic f (inbreeding coefficient) was used to test for conformity to Hardy–Weinberg equili-

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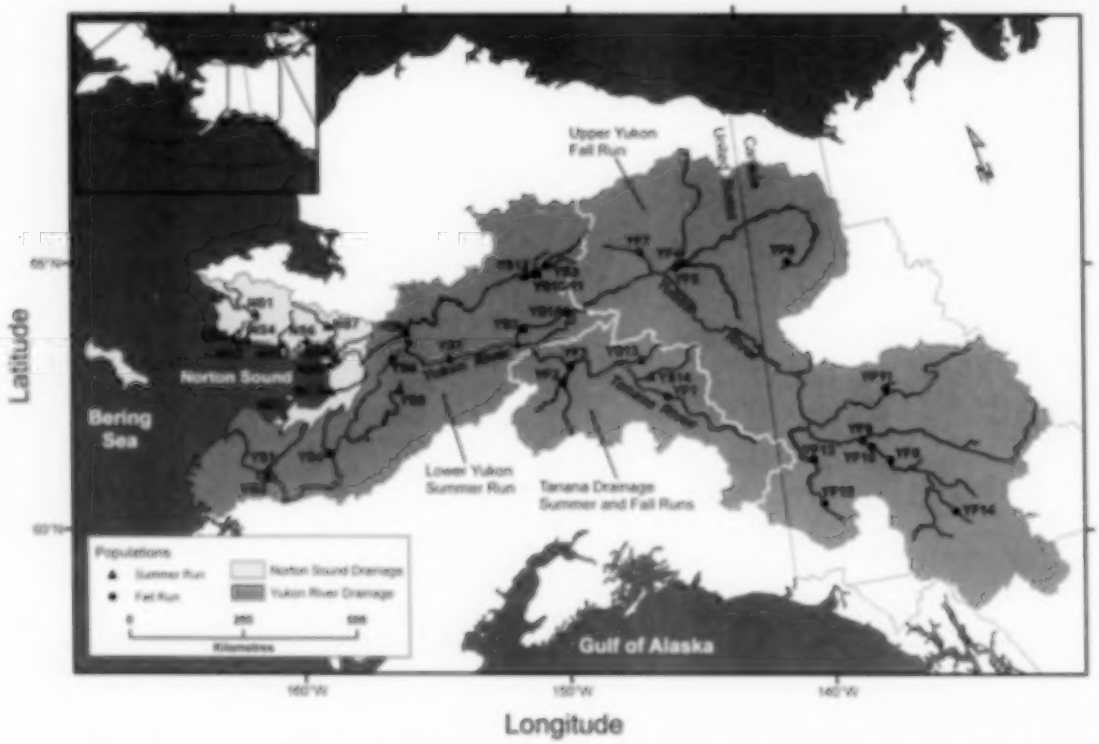
Fig. 1. Map of Alaska and Canada showing the location of chum salmon (*Oncorhynchus keta*) collections from the Norton Sound and the Yukon River.



brium (HWE) for each locus and population combination. A randomization test of the log-likelihood G statistic was used to test for genotypic disequilibrium among locus pairs over all populations. These tests were performed using FSTAT for three population groups: (*i*) Norton Sound, (*ii*) Yukon River summer run, (*iii*) Yukon River fall run. The threshold for statistical significance ($\alpha = 0.05$) was corrected (α/k) for k simultaneous tests within each population group using the sequential Bonferroni method (Rice 1989). Two values of k were used for the HWE test to evaluate each population over loci (k = number of loci) and each locus over populations (k = number of populations).

Genetic diversity among populations and population groups

An analysis of molecular variation (AMOVA) (Michalakis and Excoffier 1996) was used to estimate the level of genetic divergence over all populations (F_{st}) and determine how much variation exists within (F_{sc}) and among (F_{ct}) the three population groups. The AMOVA was performed using ARLEQUIN version 3.01 (Schneider et al. 2000), and randomization was used to test if the estimates of F_{st}, F_{sc}, and F_{ct} were significantly greater than zero. Phenetic clustering was also used to graphically depict the distribution of genetic diversity among all populations. A pairwise genetic distance matrix of the Cavalli-Sforza and Edwards (1967) chord distance (CSE) was generated from allele frequency estimates using the program GENDIST in PHYLIP version 3.5c (Felsenstein 1995). The program NEIGHBOR in PHYLIP was used to construct an unrooted neighbor-joining (NJ) phenogram based on the CSE distance matrix. The NJ phenogram was visualized using the program TreeView version 1.6.6 (Page 1996).

A G test of allelic frequency homogeneity was used to test for genetic divergence among all population pairs in each population group. Estimates of F_{st} were computed over all loci for all population pairs in each group, according to Weir and Cockerham (1984). One-sided pairwise randomization tests were used to test if estimates of mean A_r, gene diversity (H_e), and F_{st} differed between population groups. Consistent with hypothesis one, the values of A_r and H_e were expected to be comparatively high, intermediate, and low for Norton Sound, Yukon River summer-run, and Yukon River fall-run populations, respectively. The values of F_{st} were expected to be comparatively low, intermediate, and high for Norton Sound, Yukon River summer-run, and Yukon River fall-run populations, respectively. These analyses were conducted using FSTAT.

IBD pattern analysis

Mantel tests (Mantel 1967) implemented in the computer program IBD version 1.52 (Bohonak 2002) were used to test for a positive association between genetic divergence and geographic distance among populations for each of the three population groups. $F_{st}/(1 - F_{st})$ was used as the measure of genetic divergence because the populations are primarily in a linear array (Rousset 1997). The geographic distance in Norton Sound was defined as the shortest coastal route be-

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Table 1. Summary of chum salmon (*Oncorhynchus keta*) population samples collected from Norton Sound and the Yukon River.

Sample	Code	Year	*n*	EG (× 1000)
Norton Sound summer run				
Pilgrim River	NS1	2005	100	
Snake River	NS2	2005	100	1.6–2.5
Nome River	NS3	2005	100	2.9–4.3
Eldorado River	NS4	2005	100	6.0–9.2
Fish River	NS5	2005	50	
Kwiniuk River	NS6	2005	100	10–20
Koyuk River	NS7	2005	46	
Ungalik River	NS8	2005	54	
Shaktoolik River	NS9	2005	100	
Unalakleet River	NS10	2005	100	2.4–4.8
Pikmiktalik River	NS11	2005	100	
Yukon River summer run (>600 EG)				
Andreafsky River	YS1	2004	100	65–130
Chulinak River	YS2	1989	100	
Tozitna River	YS3	2002	100	
Anvik River	YS4	1988	100	350–700
California River	YS5	1997	50	
Nulato River	YS6	2003	100	
Melozitna River	YS7	2003	100	
Gisasa River (Koyukuk River)	YS8	2003	100	
Jim River (Koyukuk River)	YS9	2002	100	
South Fork Koyukuk River early	YS10	1996	100	
South Fork Koyukuk River late	YS11	1996	100	
Henshaw River (Koyukuk River)	YS12	2003	100	
Chena River (Tanana River)	YS13	1994	100	
Salcha River (Tanana River)	YS14	1994	100	
Big Salt River	YS15	2001	40	
Yukon River fall run (300–600 EG)				
Delta River (Tanana River)	YF1	1990	70	6–13
Toklat River (Tanana River)	YF2	1994	100	15–33
Kantishna River (Tanana River)	YF3	2001	100	
Sheenjek River (Porcupine River)	YF4	1989	100	50–104
Black River (Porcupine River)	YF5	1995	100	
Fishing Branch River (Porcupine River)	YF6	1997	100	>50
Chandalar River	YF7	2001	100	74–152
Tatchun River	YF8	1992	100	
Pelly River	YF9	1993	75	
Big Creek	YF10	1995	100	
Minto River	YF11	1989	100	
Kluane River (White River)	YF12	2001	100	
Donjek River (White River)	YF13	1994	65	
Teslin River	YF14	1992	100	

Note: *n*, sample size; EG, escapement goal.

tween river mouths because tagging studies have indicated returning adults likely follow the shore line (Gaudet and Schaefer 1982). The geographic distance in the Yukon River was defined as the shortest waterway route between the mouths of the tributaries that each population ascends. All distances were determined using the geographic information systems software ArcGIS (ESRI, Redlands, California). The significance of the observed Mantel test statistic (r) was determined by randomizing the data 10 000 times (Bohonak 2002).

Because of the dependencies among all population pairs used in the Mantel tests, bootstrapping was used to compare the slope (β) of the IBD regression line and the variance (σ^2) of $F_{st}/(1 - F_{st})$ between paired population groups. As the rate of gene flow increases, both β and σ^2 should decrease because the relative influence of genetic drift will decline (Hutchison and Templeton 1999). Therefore, consistent with hypothesis one, we expected both values to be smallest for the Norton Sound populations, intermediate for the Yukon River summer-run populations, and largest for the Yukon River fall-run populations. The pairwise values of $F_{st}/(1 - F_{st})$ were first restricted to those from

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Table 2. Analysis of molecular variance (AMOVA) results for chum salmon (*Oncorhynchus keta*) populations from western Alaska, including estimates of the level of genetic divergence over all populations (F_{st}) and within (F_{sc}) and among (F_{ct}) the three population groups.

Grouping strategy	Source of variation	σ^2	Percentage of total	F_{st}	F_{ct}	F_{sc}
NS–YS–YF	Total	6.866	100.00			
	Within populations	6.724	97.94			
	Among populations	0.142	2.06	0.0206*		
	Among groups	0.085	1.24		0.0124*	
	Within groups	0.057	0.83			0.0084*

Note: NS, Norton Sound; YS, Yukon River summer run; YF, Yukon River fall run. An asterisk (*) denotes the value is significantly greater than zero ($p < 0.05$).

populations within the spatial scale shared by both groups (Hutchison and Templeton 1999). A subsample of population pairs was selected via sequential random sampling, with only those population pairs composed of two populations not yet included in the subsample being considered for inclusion in the sample. Population pairs were sequentially added to the subsample until an additional pair could not be added without having a population included in the subsample twice. The result was a subsample of independent population pairs, with each population being included at most once. This approach is similar to that used by Hutchison and Templeton (1999). The slope and variance for each group were then estimated using the pairwise $F_{st}/(1 - F_{st})$ values associated with the subsample of population pairs. This subsampling process was repeated 100 000 times for each pair of groups. The test statistics were defined as the mean difference in slopes ($\Delta = \bar{\beta}_1 - \bar{\beta}_2$) and the mean variance ratio ($F = \bar{\sigma}_1^2/\bar{\sigma}_2^2$). Because the tests were one-sided (e.g., $\beta_{\text{Norton Sound}} - \beta_{\text{Yukon River summer run}} \geq 0$, $\sigma^2_{\text{Norton Sound}}/\sigma^2_{\text{Yukon River summer run}} \geq 1$), the p values were defined as the proportion of times $\beta_1 - \beta_2 < 0$ and $\sigma_1^2/\sigma_2^2 < 1$. These tests were performed using a computer program written by J. Bromaghin.

A partial Mantel test was used to evaluate the influence of seasonal run timing on genetic divergence, while controlling for the effect of geographic distance. Bivariate methods such as the partial Mantel test are appropriate here because they evaluate the influence of one indicator on pairwise estimates of genetic divergence while controlling for a second, potentially confounding indicator (Stanton et al. 1997; Hendry and Day 2005). The test was performed using IBD version 1.52 and run timing was treated as a binary variable (summer run versus fall run). The reciprocal test using geographic distance and controlling for the effect of seasonal run timing was also performed.

Results

Genetic diversity within populations

The range in genetic variation among the 20 microsatellite loci was relatively large (Appendix A; Tables A1–A3). The mean estimates of A_e and H_e over all 41 populations ranged from 1.7 (*Ole8*) to 15.9 (*Ots103*) and 0.07 (*Ole8*) to 0.94 (*Ots103*), respectively. The tests of conformity to HWE for each locus and population combination in the three groups, Norton Sound, Yukon River summer run, and Yukon River fall run, revealed 0, 3, and 5 significant results, respectively, when the α level was adjusted for multiple populations (Appendix A; Tables A1–A3). When the α level was adjusted for multiple loci, the number of significant results for Norton Sound, Yukon River summer run, and Yukon River fall run were 0, 2, and 5, respectively. These results were not common to any one locus or population. The tests for genotypic disequilibrium among locus pairs were not judged significant when the α level was adjusted for 190 pairwise tests. Allele frequencies can be obtained by contacting the corresponding author.

Genetic diversity among populations and population groups

The estimate of genetic divergence among all populations, F_{st}, was 0.021 (Table 2). The estimate of genetic divergence among the three population groups, F_{ct}, exceeded 0.012 and was larger than the estimate of genetic divergence among populations within groups ($F_{sc} = 0.008$). Each value was significantly larger than zero ($p < 0.05$). The neighbor-joining phenogram revealed a general geographic trend in the genetic grouping of populations. Populations from the same group tended to cluster together, and the Norton Sound and Yukon River fall-run populations were most distantly related (Fig. 2).

The proportion of population pairs exhibiting significant ($p < 0.05$) genotypic frequency heterogeneity was 0.67, 0.77, and 0.96 for Norton Sound, Yukon River summer-run, and Yukon River fall-run populations, respectively (Table 3). These values respectively decreased to 0.38, 0.60, and 0.90 when the α level was adjusted for simultaneous tests. The estimates of mean A_r and H_e were largest for Norton Sound, intermediate for Yukon River summer-run, and smallest for Yukon River fall-run populations (Table 4). All but the estimates of H_e for Norton Sound and Yukon River summer-run populations were significantly different ($p < 0.05$). The estimates of F_{st} over all populations were smallest for Norton Sound, intermediate for Yukon River summer-run, and largest for Yukon River fall-run populations. The estimate of F_{st} for the Yukon River fall-run populations was significantly larger ($p = 0.006$) than the estimate for the Norton Sound populations.

IBD pattern analysis

A significant ($p < 0.01$) and positive relationship between genetic divergence and geographic distance was detected for both the Yukon River summer- and fall-run populations but not for the Norton Sound populations (Fig. 3). Using the direct rather than the coastal waterway route across Norton Sound did not change the Mantel test results ($p < 0.242$) or

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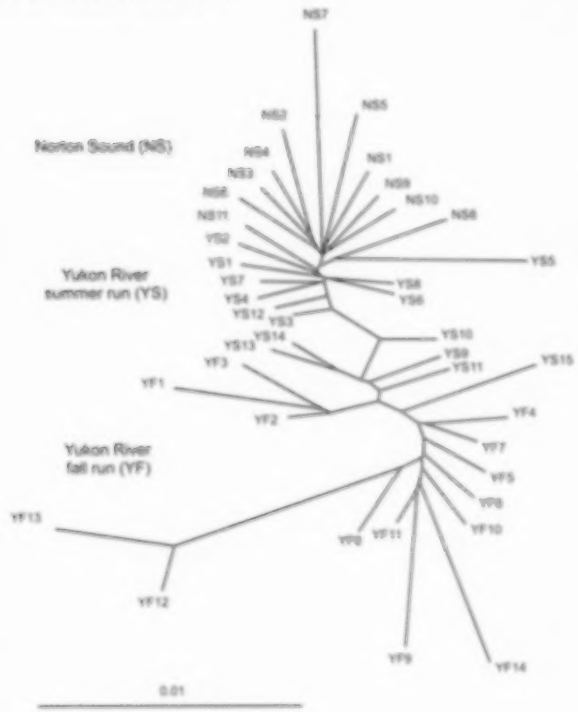
Fig. 2. Unrooted neighbor-joining phenogram for chum salmon (*Oncorhynchus keta*) from Norton Sound and the Yukon River. The phenogram was generated from the Cavalli-Sforza and Edwards (1967) chord distance for all population pairs. Sample abbreviations are as indicated in Table 1.



improve the fit of regression model ($r^2 = 0.002$). The 10 largest values of $F_{st}/(1 - F_{st})$ in Norton Sound were associated with the Koyuk River (NS7).

The one-sided pairwise tests of the slope (β) of the IBD regression line failed to reveal a significant difference between groups (Table 4). In contrast, the variance (σ^2) of $F_{st}/(1 - F_{st})$ values for the Norton Sound populations was significantly smaller ($p < 0.004$) than σ^2 for Yukon River summer- and fall-run populations. Of the latter two groups, σ^2 was significantly smaller ($p = 0.015$) in Yukon River summer-run populations.

The partial Mantel test revealed a significant ($r = 0.27$, $p < 0.001$) association between seasonal run timing and genetic divergence in Yukon River chum salmon while controlling for the effect of geographic distance (Fig. 4). However, the reciprocal test (geographic distance, controlling for the effect of seasonal run timing) was also significant ($p < 0.001$) and had a higher test statistic ($r = 0.45$). The pairwise estimates of genetic divergence between populations of different run timing overlapped with those of populations exhibiting the same run timing when examined at the same spatial scale (0–1200 km).

Discussion

The objective of this study was to test hypotheses regarding the influence of hydrographic structure and seasonal run timing on gene flow in western Alaska chum salmon. Relational differences (i.e., greater than, less than) in gene flow were inferred from comparative analyses of gene diversity and IBD patterns. We discuss the results with respect to each hypothesis below.

H_1: gene flow is comparatively high, medium, and low for Norton Sound, Yukon River summer-run, and Yukon River fall-run populations, respectively

Norton Sound

The estimates of genetic diversity and IBD patterns suggest gene flow is highest in Norton Sound. The Norton Sound populations generally had significantly higher intrapopulation diversity (A_r, H_s), lower interpopulation diversity (F_{st}), and smaller variance in pairwise $F_{st}/(1 - F_{st})$ values than the two groups from the Yukon River. In addition, the failure to detect IBD in Norton Sound suggests gene flow is sufficiently strong that little differentiation exists, regardless of the amount of spatial separation (case II pattern, Hutchison and Templeton 1999). The benefits of dispersal may be greater in Norton Sound because the smaller populations may be more sensitive to extreme declines in abundance. For example, the recent declines of western Alaska chum salmon populations impacted Norton Sound to a much greater degree than the Yukon River, resulting in more populations designated as "yield concerns" (chronic inability to maintain a harvestable surplus despite specific management measure) than anywhere in the state of Alaska (Menard 2003). These smaller populations may be indicative of low and more variable habitat quality that could favor greater dispersal in response to greater extinction risk compared with the Yukon River (Hanski and Gilpin 1997; Hendry et al. 2004). In fact, the lack of IBD suggests chum salmon in Norton Sound may function more as a metapopulation (e.g., Garant et al. 2000).

On the other hand, the benefits of philopatry are likely greater for both groups of chum salmon in the Yukon River compared with Norton Sound. The Yukon River watershed is composed of 20 ecoregions compared with two for the Norton Sound watershed (Brabets et al. 2000). The greater broadscale habitat heterogeneity in the Yukon River may promote adaptation to the local conditions, which in turn benefits philopatric individuals more so than in Norton Sound (Hendry et al. 2004). Also, the freshwater migration is much longer for most Yukon River populations (mean ~1200 km) compared with Norton Sound populations (mean river length ~110 km). A longer freshwater migration in a large riverine system increases the navigational complexity and, theoretically, the cost of dispersal (Hendry et al. 2004).

Some results were equivocal or revealed unique patterns. First, the estimates of H_s and F_{st} for Norton Sound were not significantly different from the corresponding values for the Yukon River summer-run populations. The failure to detect statistically significant differences for these two parameters may be a function of statistical power. Rare alleles can be lost with little change in heterozygosity (Luikart and Cornuet 1998), which may explain why only the A_r values were significantly different. Second, the slope of the IBD linear

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Table 3. A matrix of F_{st} (below diagonal) and G test p values (above diagonal) for samples from Norton Sound and the Yukon River.

(*a*) Norton Sound.

	NS1	NS2	NS3	NS4	NS5	NS6	NS7	NS8	NS9	NS10	NS11
NS1	—	**0.0009**	0.0027	0.0073	0.4146	**0.0009**	**0.0009**	0.0864	0.0018	0.0418	**0.0009**
NS2	0.0035	—	0.0036	**0.0009**	**0.0009**	**0.0009**	**0.0009**	**0.0009**	**0.0009**	**0.0009**	**0.0009**
NS3	0.0013	0.0011	—	0.2927	0.5609	0.1455	**0.0009**	0.5382	0.4418	0.2409	0.0036
NS4	0.0025	0.0014	−0.0008	—	0.0527	0.0055	**0.0009**	0.1200	0.0027	0.0036	**0.0009**
NS5	0.0008	0.0035	0.0002	0.0007	—	0.1282	0.0055	0.4636	0.5227	0.4591	0.0027
NS6	0.0024	0.0033	0.0001	0.0023	0.0018	—	**0.0009**	0.0773	0.0191	**0.0009**	**0.0009**
NS7	0.0066	0.0103	0.0080	0.0087	0.0054	0.0096	—	0.0018	**0.0009**	**0.0009**	**0.0009**
NS8	0.0010	0.0037	−0.0005	0.0011	0.0011	0.0019	0.0076	—	0.4236	0.3700	0.0473
NS9	0.0014	0.0021	−0.0008	0.0011	0.0004	0.0001	0.0080	0.0011	—	0.2473	0.0382
NS10	0.0016	0.0040	−0.0003	0.0010	0.0011	0.0017	0.0088	0.0012	0.0002	—	0.0436
NS11	0.0025	0.0045	0.0010	0.0023	0.0024	0.0025	0.0097	0.0012	0.0005	0.0010	—

(*b*) Yukon River summer run.

	YS1	YS2	YS3	YS4	YS5	YS6	YS7	YS8	YS9	YS10	YS11	YS12	YS13	YS14	YS15
YS1	—	0.0129	0.0671	0.0310	0.0057	0.0729	0.2391	0.0986	**0.0005**	**0.0005**	**0.0005**	0.0138	**0.0005**	**0.0005**	**0.0005**
YS2	0.0009	—	0.0076	0.5638	0.0019	0.0671	0.1829	0.0657	**0.0005**	**0.0005**	**0.0005**	0.0262	**0.0005**	**0.0005**	**0.0005**
YS3	0.0014	0.0011	—	0.0619	**0.0005**	0.3043	0.0276	0.1081	**0.0005**	0.0010	**0.0005**	0.1971	**0.0005**	**0.0005**	**0.0005**
YS4	0.0012	0.0004	0.0009	—	**0.0005**	0.9191	0.8971	0.3938	**0.0005**	**0.0005**	**0.0005**	0.5138	**0.0005**	**0.0005**	**0.0005**
YS5	0.0034	0.0033	0.0052	0.0061	—	0.0014	**0.0005**	**0.0005**	**0.0005**	**0.0005**	**0.0005**	**0.0005**	**0.0005**	**0.0005**	**0.0005**
YS6	0.0004	0.0008	0.0010	−0.0006	0.0038	—	0.1805	0.6448	**0.0005**	**0.0005**	**0.0005**	0.0576	**0.0005**	**0.0005**	**0.0005**
YS7	0.0001	−0.0009	0.0007	−0.0001	0.0038	−0.0003	—	0.2981	**0.0005**	**0.0005**	**0.0005**	0.2395	**0.0005**	**0.0005**	**0.0005**
YS8	0.0007	0.0007	0.0009	−0.0005	0.0047	−0.0004	−0.0004	—	**0.0005**	**0.0005**	**0.0005**	0.0324	**0.0005**	**0.0005**	**0.0005**
YS9	0.0146	0.0149	0.0084	0.0138	0.0197	0.0153	0.0131	0.0157	—	**0.0005**	0.0029	**0.0005**	0.0033	0.0024	0.0514
YS10	0.0064	0.0076	0.0038	0.0067	0.0110	0.0062	0.0054	0.0080	0.0054	—	0.0010	0.0838	0.0014	**0.0005**	0.0114
YS11	0.0149	0.0155	0.0084	0.0119	0.0199	0.0144	0.0139	0.0149	0.0036	0.0045	—	**0.0005**	**0.0005**	**0.0005**	0.0129
YS12	0.0008	0.0008	0.0003	0.0003	0.0061	0.0004	−0.0006	0.0010	0.0112	0.0034	0.0099	—	**0.0005**	**0.0005**	**0.0005**
YS13	0.0156	0.0154	0.0085	0.0159	0.0204	0.0161	0.0135	0.0158	0.0029	0.0046	0.0070	0.0111	—	0.8014	**0.0005**
YS14	0.0149	0.0136	0.0077	0.0137	0.0186	0.0141	0.0110	0.0131	0.0029	0.0033	0.0051	0.0094	0.0002	—	**0.0005**
YS15	0.0154	0.0163	0.0080	0.0112	0.0174	0.0138	0.0141	0.0153	0.0034	0.0063	0.0016	0.0106	0.0091	0.0084	—

(*c*) Yukon River fall run.

	YF1	YF2	YF3	YF4	YF5	YF6	YF7	YF8	YF9	YF10	YF11	YF12	YF13	YF14
YF1	—	**0.0006**	**0.0006**	**0.0006**	**0.0006**	**0.0006**	**0.0006**	**0.0006**	**0.0006**	**0.0006**	**0.0006**	**0.0006**	**0.0006**	**0.0006**
YF2	0.0042	—	0.0017	**0.0006**	**0.0006**	**0.0006**	**0.0006**	**0.0006**	**0.0006**	**0.0006**	**0.0006**	**0.0006**	**0.0006**	**0.0006**
YF3	0.0062	0.0020	—	**0.0006**	**0.0006**	**0.0006**	**0.0006**	**0.0006**	**0.0006**	**0.0006**	**0.0006**	**0.0006**	**0.0006**	**0.0006**
YF4	0.0143	0.0154	0.0157	—	**0.0006**	**0.0006**	0.0440	**0.0006**	**0.0006**	**0.0006**	**0.0006**	**0.0006**	**0.0006**	**0.0006**
YF5	0.0144	0.0153	0.0182	0.0021	—	**0.0006**	**0.0006**	0.0148	**0.0006**	**0.0006**	**0.0006**	**0.0006**	**0.0006**	**0.0006**
YF6	0.0169	0.0151	0.0181	0.0064	0.0038	—	**0.0006**	**0.0006**	**0.0006**	**0.0006**	**0.0006**	**0.0006**	**0.0006**	**0.0006**
YF7	0.0084	0.0086	0.0110	0.0008	0.0021	0.0052	—	**0.0006**	**0.0006**	**0.0006**	**0.0006**	**0.0006**	**0.0006**	**0.0006**
YF8	0.0105	0.0144	0.0163	0.0038	0.0013	0.0057	0.0023	—	**0.0006**	0.1181	0.7264	**0.0006**	**0.0006**	**0.0006**
YF9	0.0108	0.0145	0.0171	0.0075	0.0065	0.0082	0.0041	0.0024	—	0.0440	0.3379	**0.0006**	**0.0006**	**0.0006**
YF10	0.0103	0.0131	0.0133	0.0049	0.0051	0.0055	0.0038	0.0012	0.0011	—	0.8643	**0.0006**	**0.0006**	**0.0006**
YF11	0.0101	0.0128	0.0132	0.0036	0.0035	0.0052	0.0029	−0.0007	0.0012	−0.0003	—	**0.0006**	**0.0006**	**0.0006**
YF12	0.0282	0.0297	0.0293	0.0246	0.0219	0.0218	0.0220	0.0212	0.0253	0.0193	0.0240	—	0.0137	**0.0006**
YF13	0.0288	0.0296	0.0299	0.0303	0.0290	0.0271	0.0270	0.0262	0.0283	0.0231	0.0259	0.0028	—	**0.0006**
YF14	0.0237	0.0230	0.0235	0.0197	0.0200	0.0195	0.0162	0.0134	0.0168	0.0124	0.0095	0.0431	0.0443	—

Note: Sample abbreviations are as indicated in Table 1. Bold p values were judged significant after adjusting α for multiple tests.

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Table 4. Pairwise comparison of genetic diversity and the isolation-by-distance (IBD) pattern between chum salmon (*Oncorhynchus keta*) groups.

	H_0 genetic diversity			H_0 IBD	
Pairs	$A_{r_1} \geq A_{r_2}$	$H_{e_1} \geq H_{e_2}$	$F_{st_1} \geq F_{st_2}$	$\Delta \geq 0$	$F \geq 1$
1. NS	9.0	0.682	0.002	—	—
2. YS	8.3	0.677	0.007	> -0.0001	0.311
p	0.026	0.228	0.166	0.190	0.003
1. NS	9.0	0.682	0.002	—	—
2. YF	7.2	0.657	0.014	> -0.0001	0.101
p	0.002	0.002	0.006	0.111	<0.001
1. YS	8.3	0.677	0.007	—	—
2. YF	7.2	0.657	0.014	> -0.0001	0.409
p	0.002	0.002	0.072	0.368	0.015

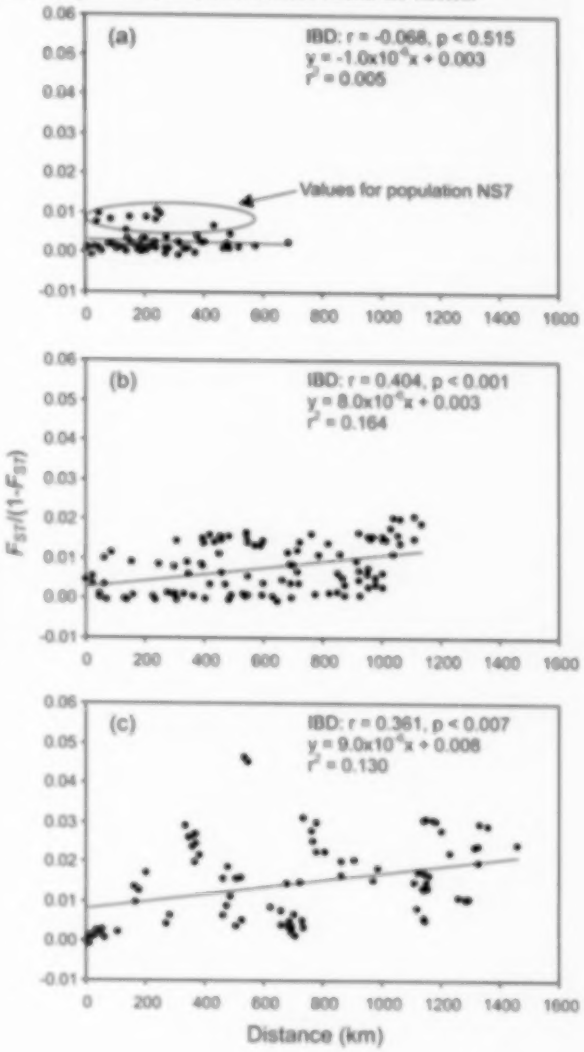
Note: H_0, the null hypothesis; A_r, allelic richness; H_e, mean heterozygosity; F_{st}, level of genetic divergence over all populations; Δ, mean difference in slope (group 1 – group 2) of linear regression; F, mean ratio of variances (group 1/group 2) of pairwise $F_{st}/(1 - F_{st})$; NS, Norton Sound; YS, Yukon River summer run; YF, Yukon River fall run. Subscripts 1 and 2 refer to the population number in each pairwise comparison.

regression for Norton Sound was not significantly different from the two Yukon River groups. This result likely reflects the high variation in pairwise $F_{st}/(1 - F_{st})$ values in the Yukon River. Finally, the IBD plot revealed a unique population in Norton Sound. The 10 largest pairwise values of $F_{st}/(1 - F_{st})$ were associated with the Koyuk River population (NS7). These results may reflect local gene-flow heterogeneity associated with tributary-level hydrographic structure and life history. The Koyuk River is the longest river (259 km) in Norton Sound (50% longer than the next in length), and Koyuk River chum salmon may also spawn somewhat later than other Norton Sound chum salmon (C. Lean, P.O. Box 358, Nome, AK 99762, USA, personal communication).

Yukon River

The estimates of genetic diversity and IBD patterns suggest gene flow is higher among the summer-run than fall-run populations. The summer-run populations had significantly higher intrapopulation diversity and smaller variance in pairwise $F_{st}/(1 - F_{st})$ values than the fall-run populations. IBD was detected in both groups. Evaluating these results in terms of fitness costs and benefits suggest the costs of dispersal (and benefits of philopatry) are generally greater for upstream, fall-run populations. For example, the longer freshwater migration required of most fall-run populations (mean ~1700 km) is more complex than for most summer-run populations (mean ~860 km), increasing the cost of dispersal and favoring philopatry (Hendry et al. 2004). More ecoregions occur in the upper drainage occupied by fall-run populations (19) than in the lower drainage occupied by summer-run populations (7), which may result in greater local adaptation and favor stronger philopatry for the former (Hendry et al. 2004). The results also suggest that gene flow for some summer-run populations nearer the Yukon River mouth (e.g., YS1–YS4, YS6–YS8) may be more similar to Norton Sound populations than to summer-run populations further up the drainage. The pairwise estimates of $F_{st}/(1 - F_{st})$ among these seven populations

Fig. 3. Scatterplots of genetic divergence versus geographic distance for (*a*) Norton Sound chum salmon (*Oncorhynchus keta*), (*b*) Yukon River summer-run chum salmon, and (*c*) Yukon River fall-run chum salmon. The test statistic (*r*) and *p* value are shown for the Mantel test of isolation-by-distance (IBD). The linear regression line, least-squares equation, and correlation coefficient (r^2) are also shown. The 10 pairwise values associated with the Koyuk River population (NS7) from Norton Sound are circled.



(mean < 0.001) fall below the linear regression line in Fig. 2, consistent with higher relative gene flow (Koizumi et al. 2006). In contrast, the pairwise estimates of $F_{st}/(1 - F_{st})$ among the other eight populations (mean > 0.008) fall equally above and below the linear regression line, consistent with lower relative gene flow.

Considering genetic drift

The results discussed above could also reflect comparatively lower, intermediate, and higher rates of genetic drift

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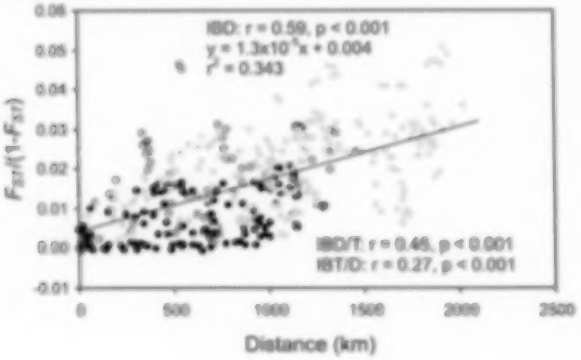
Fig. 4. Scatterplot of genetic divergence versus geographic distance for chum salmon (*Oncorhynchus keta*) from the Yukon River (black circle = summer–summer, open circle = fall–fall, grey circle = summer–fall). The test statistic (r) and p value are shown for the Mantel test of isolation-by-distance (IBD) over all population pairs and for the partial Mantel test, controlling for run time (IBD–T) and geographic distance (IBT–D). The linear regression line, least-squares equation, and correlation coefficient (r^2) represent all population pairs.



for Norton Sound, Yukon River summer-run, and Yukon River fall-run populations, respectively. However, we feel it is unlikely that genetic drift alone could result in the trend and magnitude of difference in the estimates of diversity and IBD patterns. In fact, the rate of genetic drift is likely to be highest in Norton Sound populations because census estimates and escapement goals indicate they are much smaller than most Yukon River populations (Brannian et al. 2006). Within the Yukon River, the drainage-wide optimum escapement goals for summer-run (600 000) and fall-run (300 000) chum salmon indicate the former are more abundant (Bue et al. 2006; Clark et al. 2006). However, this difference is largely due to a single summer-run population, Anvik River (YS4), in the lower Yukon River. The census data indicate many summer- and fall-run populations are similar in size and thus likely have similar rates of genetic drift.

The Yukon River population samples were collected as much as 16 years apart. Genetic drift resulting from this temporal variation, if sufficiently strong, could also bias our conclusions. To assess this possibility, we tested for a significant relationship between pairwise estimates of F_{st} and the number of years between samples in both the Yukon River summer- and fall-run population groups. Because genetic drift is a diversifying force, we would expect there to be a positive relationship between F_{st} and the years between samples if the rate of genetic drift is sufficiently strong. However, Mantel tests (IBD version 1.52) failed to reveal a positive relationship for either the summer-run ($r^2 < 0.001$, $p = 0.554$) or fall-run ($r^2 < 0.001$, $p = 0.528$) populations. In fact, some of the lowest F_{st} values occurred between samples collected 14–16 years apart (see pairwise F_{st} values for population YS4). We believe these results indicate that our conclusions are unlikely to be biased by genetic drift because the temporal scale (of sample collections) is too short, the populations are too large, or both (Nei and Chakravarti 1977). This conclusion is further supported by studies of Chinook salmon (*Oncorhynchus tshawytscha*) and sockeye salmon (*Oncorhynchus nerka*) that indicate differences in sample collection dates of as much as 20 years contribute little to the overall estimates of interpopulation genetic diversity (Beacham et al. 2006*a*, 2006*b*). We were unable to find comparable studies of chum salmon.

H_2: genetic divergence in Yukon River chum salmon is influenced by seasonal run timing

The partial Mantel test results support hypothesis two. Genetic divergence among Yukon River chum salmon was associated with seasonal run timing (isolation-by-time) when controlling for the effect of geographic distance. Importantly, though, the reciprocal test was also true. Seasonal variation in timing of adult returns has been shown to contribute to genetic differentiation of sympatric populations of Pacific salmon (e.g., Fillatre et al. 2003; Ramstad et al. 2003). These studies demonstrate that run timing need not be discontinuous for some reproductive isolation to occur. Our results, however, suggest that run-timing variation does not necessarily prevent gene flow, consistent with the findings of Coulson et al. (2006) for anadromous rainbow smelt (*Osmerus mordax*). In fact, the level of differentiation among proximate population pairs with opposing run timing is similar to that of some proximate population pairs with the same run timing. These results appear to conflict with the observed differences in spawning habitat (Maclean 2003). One explanation for this is that the selective forces associated with spawning habitat are not strong enough to completely prevent gene flow during the period of time when the runs overlap. For example, the temperature regimes in the upwelling (fall run) and downwelling (summer run) areas in the Tanana River exhibit different norms (Maclean 2003); however, intra- and inter-annual variation (particularly in the downwelling habitat) likely afford some reproductive success for alternative run-time immigrants. Similarly, Fillatre et al. (2003) found that life-history differences between sympatric but seasonal runs of sockeye salmon have a strong environmental component and concluded some gene flow occurs between the two runs despite being genetically differentiated.

Implications for gene flow and conservation

Our conclusions regarding the influence of hydrographic structure on intraspecific gene flow are consistent with comparisons among Pacific salmon species as well as studies of other salmonids. For example, Quinn (2005) hypothesized that species like pink salmon (*Oncorhynchus gorbuscha*) that typically spawn in short, relatively unstable coastal streams should exhibit higher gene flow compared with other Pacific salmon species that undergo longer freshwater migrations. Estimates of genetic divergence are consistent with this hypothesis (Hendry et al. 2004). Hébert et al. (2000) examined the influence of hydrographic structure on genetic diversity in brook trout (*Salvelinus fontinalis*). Although their results were equivocal for estimates of intrapopulation genetic diversity, populations from the least physically complex system exhibited statistically significant lower genetic divergence as predicted given the potential for higher gene flow.

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The results from this study suggest that the complexity of the hydrographic system may influence population resilience and the spatial scale required for conservation of these western Alaska chum salmon populations. For example, evidence of comparatively high intrapopulation diversity and no IBD in Norton Sound, a nonhierarchical collection of coastal rivers, suggests relatively high gene flow among all populations may help ensure population resilience despite the relatively small size of populations. Thus, maintaining connectivity among all populations should be an important consideration when evaluating conservation priorities for Norton Sound. On the other hand, evidence of IBD within the Yukon River, a long network of inland tributaries, suggests gene flow there is more important locally among neighboring populations that more likely share similar selective regimes. Defining a single spatial scale for conservation (e.g., Primmer et al. 2006) does not seem possible given the inferred gene-flow heterogeneity and the fact that the two seasonal runs are not genetically isolated. Rather, the spatial scale for conservation is likely to decrease with distance from the mouth and generally be smaller for fall-run than for summer-run populations given that the former tend to be more isolated (Flannery et al. 2007).

We have argued that the inferred gene-flow differences are adaptive; however, it is important to point out that geographic location may partly explain the differences. Under the geographic location argument, the rate of gene flow within the three groups is related to their relative isolation. For example, the Norton Sound populations are the least isolated, so they are most likely to receive immigrants from the other two groups. Although we do not refute this alternative explanation, we think that the physical distinctions between the two watersheds make it unreasonable to conclude location alone is influencing gene flow. For example, it seems highly unlikely that fall-run chum salmon from the upper Yukon River will stray and spawn in Norton Sound given the order-of-magnitude difference in migration distance. In addition, the geographic coherence of the neighbor-joining phenogram and the fact that F_{CT} (among group genetic divergence) exceeded F_{SC} (within group genetic divergence) suggest gene flow is limited among, relative to within, groups.

Finally, it is also important to note that further analysis is needed to generalize conclusions regarding the influence of hydrographic structure on gene flow in Pacific salmon. The present study test a priori predictions based on ecological theory; however, it is a case study with a single representative of the two hydrographic systems: coastal rivers (Norton Sound) and inland tributaries (Yukon River). An examination of other coastal and inland systems will provide the needed replication to confirm the present results and generalize the conclusions.

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Appendix A

Tables A1–A3 appear on the following pages.

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Table A1. Genetic diversity at 20 microsatellite loci in chum salmon (*Oncorhynchus keta*) population samples from Norton Sound (NS).

	Population										
Locus	NS1	NS2	NS3	NS4	NS5	NS6	NS7	NS8	NS9	NS10	NS11
Oki23											
n	90	87	89	92	48	88	42	48	93	86	91
H_e	0.25	0.21	0.18	0.18	0.28	0.25	0.29	0.17	0.26	0.24	0.31
H_o	0.23	0.23	0.19	0.16	0.31	0.25	0.24	0.19	0.29	0.23	0.34
A_r	2.6	2.7	2.6	2.8	2.9	3.1	2.6	2.3	3.1	2.7	2.9
Oke8											
n	89	86	89	90	48	88	42	47	92	85	89
H_e	0.07	0.08	0.07	0.05	0.08	0.08	0.05	0.10	0.10	0.12	0.16
H_o	0.07	0.08	0.07	0.06	0.08	0.08	0.05	0.11	0.11	0.11	0.15
A_r	1.8	2.0	1.8	1.6	1.8	1.8	1.6	1.9	1.9	1.9	2.0
Oke3											
n	85	85	88	88	46	86	40	47	89	80	84
H_e	0.77	0.79	0.74	0.76	0.75	0.74	0.73	0.75	0.78	0.73	0.75
H_o	0.76	0.79	0.77	0.75	0.76	0.76	0.73	0.83	0.79	**0.64**	0.80
A_r	5.9	5.8	5.9	6.2	5.3	5.4	5.1	6.4	6.5	6.1	6.0
Oke4											
n	87	86	88	89	46	78	40	46	86	81	85
H_e	0.07	0.20	0.13	0.17	0.15	0.10	0.10	0.08	0.12	0.10	0.02
H_o	0.07	0.17	0.14	0.18	0.15	0.10	0.10	0.09	0.13	0.07	0.02
A_r	1.9	2.7	2.3	2.5	2.8	2.1	2.3	1.8	2.4	2.2	1.3
Ots2.1L											
n	89	88	90	92	48	87	42	48	94	85	85
H_e	0.11	0.11	0.10	0.14	0.17	0.11	0.18	0.12	0.09	0.11	0.10
H_o	0.11	0.11	0.10	0.15	0.19	0.11	0.14	0.13	0.10	0.09	0.11
A_r	1.9	1.9	1.8	1.9	2.0	1.9	2.0	1.9	1.8	1.9	1.9
Ots2.1U											
n	87	88	88	87	48	84	42	47	95	84	83
H_e	0.62	0.61	0.61	0.61	0.58	0.57	0.52	0.63	0.57	0.57	0.57
H_o	0.67	0.61	0.53	0.59	0.67	0.55	0.55	**0.51**	0.58	0.55	0.57
A_r	3.6	3.0	4.1	3.2	3.7	3.4	3.4	4.6	3.5	3.9	3.6
Oke11											
n	88	88	88	86	47	78	41	46	88	79	86
H_e	0.47	0.57	0.61	0.59	0.61	0.52	0.56	0.49	0.55	0.61	0.51
H_o	0.49	0.51	0.59	0.60	0.55	0.50	**0.41**	0.50	**0.48**	0.53	0.45
A_r	4.6	5.1	5.3	4.9	4.6	4.3	5.1	4.4	4.8	4.8	4.5
Ots103											
n	88	88	80	89	45	83	33	48	81	83	88
H_e	0.94	0.94	0.95	0.94	0.95	0.94	0.95	0.95	0.95	0.95	0.95
H_o	0.97	0.95	0.93	0.94	0.96	0.93	1.00	0.98	0.96	0.93	0.95
A_r	16.7	15.9	17.4	16.0	17.6	16.3	17.8	18.1	16.9	17.8	18.0
Oki1L											
n	90	88	89	92	45	82	43	49	94	86	92
H_e	0.37	0.34	0.38	0.42	0.42	0.31	0.49	0.41	0.33	0.41	0.41
H_o	0.33	0.38	0.43	**0.33**	0.44	0.33	0.60	0.39	0.33	0.41	0.39
A_r	2.6	2.5	2.8	2.7	2.7	2.8	2.9	2.3	2.7	2.6	2.5
Oki1U											
n	88	89	84	88	45	79	41	48	92	83	88
H_e	0.92	0.90	0.92	0.92	0.92	0.89	0.91	0.91	0.92	0.92	0.92
H_o	0.90	0.85	0.90	0.90	0.89	0.89	0.98	0.98	0.91	0.93	0.94
A_r	12.8	12.0	12.8	11.9	12.8	11.1	12.6	12.0	13.3	13.2	12.7
Oki100											
n	91	90	88	93	48	88	43	49	93	87	91
H_e	0.90	0.91	0.92	0.90	0.92	0.92	0.89	0.90	0.90	0.89	0.91
H_o	0.93	0.92	0.94	0.92	0.94	0.86	0.84	0.84	0.85	0.92	0.92
A_r	12.2	12.7	14.0	13.3	14.0	13.1	12.0	12.3	12.4	13.0	12.9

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Table A1 *(concluded).*

	Population										
Locus	NS1	NS2	NS3	NS4	NS5	NS6	NS7	NS8	NS9	NS10	NS11
Oki2											
n	87	88	89	91	45	85	42	48	90	86	91
H_e	0.89	0.88	0.90	0.90	0.89	0.90	0.91	0.88	0.91	0.90	0.90
H_o	0.91	0.89	0.87	0.90	0.89	0.87	0.95	0.85	0.87	0.90	0.87
A_r	10.3	9.6	10.9	10.3	10.4	10.8	10.4	10.6	10.5	11.0	9.8
Omy101											
n	90	91	89	93	48	86	43	49	94	86	91
H_e	0.90	0.94	0.92	0.93	0.93	0.94	0.87	0.92	0.93	0.92	0.91
H_o	0.89	0.92	0.93	0.94	1.00	0.90	0.88	0.94	0.94	0.93	0.89
A_r	14.2	15.3	14.5	14.5	14.8	15.6	12.2	14.4	15.2	14.2	13.4
One101											
n	91	88	89	91	47	87	41	49	95	86	90
H_e	0.90	0.88	0.91	0.90	0.89	0.89	0.83	0.92	0.91	0.90	0.92
H_o	**0.84**	0.92	0.88	0.89	0.98	0.92	0.76	0.98	0.88	0.90	0.90
A_r	13.7	12.4	13.7	13.8	13.1	13.1	11.5	13.8	13.7	13.7	14.2
One102											
n	90	91	90	89	48	80	41	47	95	84	91
H_e	0.91	0.90	0.91	0.91	0.89	0.90	0.92	0.91	0.91	0.92	0.91
H_o	**0.84**	0.89	0.93	**0.83**	0.90	0.86	0.88	0.96	0.88	0.88	0.89
A_r	12.1	11.6	12.0	11.3	10.5	10.3	12.3	11.7	11.2	12.1	11.9
One104											
n	90	90	90	93	46	87	36	47	94	81	91
H_e	0.93	0.94	0.94	0.94	0.95	0.94	0.91	0.93	0.93	0.93	0.93
H_o	0.94	0.94	0.89	0.95	0.96	0.98	0.97	0.96	0.94	0.98	0.92
A_r	15.1	15.0	15.4	15.6	16.2	14.7	14.0	14.7	14.4	14.9	15.3
One114											
n	90	88	89	93	48	87	43	49	94	86	87
H_e	0.93	0.92	0.93	0.93	0.93	0.92	0.92	0.92	0.93	0.93	0.93
H_o	0.91	0.92	0.98	0.97	0.90	0.95	0.95	0.92	**0.87**	0.94	0.92
A_r	14.1	13.0	14.8	13.9	13.8	13.5	13.9	12.8	13.5	14.1	13.6
Otv3											
n	90	91	88	93	47	81	41	49	95	85	90
H_e	0.73	0.79	0.77	0.77	0.71	0.79	0.80	0.75	0.78	0.76	0.77
H_o	0.66	0.79	0.77	0.78	0.72	0.78	0.76	0.88	0.80	0.78	0.72
A_r	7.3	8.5	8.1	7.6	7.6	8.9	8.6	8.2	8.5	7.5	7.4
Otvg68											
n	90	91	89	92	48	86	43	49	93	85	90
H_e	0.95	0.94	0.95	0.95	0.94	0.95	0.95	0.93	0.94	0.94	0.94
H_o	0.96	0.95	0.96	0.96	0.98	0.92	0.93	0.92	0.97	0.95	0.96
A_r	17.4	16.6	18.2	17.6	17.7	17.0	17.5	17.7	17.0	16.2	16.4
Sssa419											
n	90	90	90	93	48	88	43	48	93	86	89
H_e	0.85	0.87	0.85	0.85	0.86	0.88	0.87	0.87	0.86	0.83	0.87
H_o	0.86	0.90	0.80	0.85	0.85	**0.80**	0.81	0.81	0.88	**0.74**	0.88
A_r	8.6	9.5	9.1	8.9	8.5	10.6	9.0	9.4	9.2	8.3	10.1
Average											
n	89	89	88	91	47	84	41	48	92	84	89
H_e	0.67	0.69	0.68	0.69	0.69	0.68	0.68	0.68	0.68	0.68	0.68
H_o	0.67	0.69	0.68	0.68	0.71	0.67	0.68	0.69	0.68	0.67	0.68
A_r	9.0	8.9	9.4	9.0	9.1	9.0	8.8	9.1	9.1	9.1	9.0

Note: Sample abbreviations are as indicated in Table 1. A bold value indicates that the sample–locus does not conform to Hardy–Weinberg expectation ($p < 0.05$). Allelic richness (A_r) estimates are based on a minimum sample size of 33 diploid individuals. *n*, sample size; H_e, expected heterozygosity; H_o, observed heterozygosity.

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Table A2. Genetic diversity at 20 microsatellite loci in summer-run chum salmon (*Oncorhynchus keta*) population samples from the Yukon River (YS).

	Population														
Locus	YS1	YS2	YS3	YS4	YS5	YS6	YS7	YS8	YS9	YS10	YS11	YS12	YS13	YS14	YS15
Oki23															
n	100	88	100	89	42	93	100	100	100	85	91	100	98	98	39
H_e	0.31	0.34	0.36	0.28	0.30	0.21	0.32	0.33	0.47	0.35	0.40	0.26	0.45	0.46	0.36
H_o	0.29	**0.28**	0.37	0.30	0.33	0.19	0.34	0.37	0.53	0.32	0.43	0.24	0.41	0.45	0.38
A_r	2.9	3.1	2.7	2.6	2.9	2.5	2.9	2.9	3.0	2.6	2.9	2.5	2.9	3.0	2.9
Oke8															
n	100	89	100	89	43	92	100	99	100	85	91	100	96	97	37
H_e	0.10	0.11	0.10	0.17	0.09	0.09	0.11	0.11	0.07	0.06	0.11	0.10	0.07	0.05	0.08
H_o	0.11	0.09	0.11	0.19	0.09	0.10	0.12	0.11	0.07	0.06	0.10	0.11	0.07	0.05	**0.03**
A_r	1.9	1.9	1.9	2.0	1.9	1.8	1.9	1.9	1.7	1.7	1.9	1.9	1.7	1.6	1.8
Oke3															
n	100	89	63	88	39	80	99	94	100	85	90	100	90	95	33
H_e	0.74	0.72	0.72	0.75	0.73	0.73	0.73	0.75	0.60	0.71	0.61	0.74	0.64	0.62	0.61
H_o	0.75	0.75	**0.62**	0.69	0.74	0.76	0.76	0.74	0.59	0.71	0.58	0.78	0.62	0.69	0.64
A_r	5.4	5.5	5.2	5.4	6.1	5.3	5.4	5.8	3.9	5.2	3.9	5.3	4.3	4.0	3.9
Oke4															
n	100	89	98	88	29	79	100	96	100	85	91	100	93	88	35
H_e	0.12	0.11	0.16	0.09	0.03	0.09	0.07	0.14	0.17	0.11	0.14	0.13	0.17	0.14	0.19
H_o	0.10	0.11	0.14	0.09	0.03	0.09	0.06	0.15	0.18	0.11	0.13	0.14	0.18	0.15	0.20
A_r	2.4	1.9	2.2	2.1	1.6	2.0	1.9	2.4	2.6	2.2	2.4	2.2	2.0	2.1	2.4
Ots2.1L															
n	100	89	100	88	45	93	100	100	100	84	89	100	89	97	38
H_e	0.10	0.07	0.17	0.12	0.16	0.10	0.14	0.07	0.17	0.10	0.15	0.17	0.13	0.09	0.25
H_o	0.11	0.07	0.15	0.10	0.18	0.11	0.15	0.07	0.16	0.08	0.16	0.18	0.13	0.09	0.29
A_r	1.9	1.7	2.0	1.9	2.0	1.9	1.9	1.7	2.0	1.9	1.9	2.0	1.9	1.8	2.0
Ots2.1U															
n	100	89	100	88	43	93	100	100	100	85	86	100	85	96	39
H_e	0.56	0.56	0.57	0.55	0.61	0.59	0.58	0.58	0.56	0.54	0.58	0.54	0.51	0.56	0.57
H_o	**0.47**	0.56	0.62	0.51	0.53	0.56	**0.49**	0.58	0.52	0.54	0.57	0.55	0.48	0.56	0.49
A_r	3.5	3.0	3.2	3.4	3.0	3.2	3.2	3.2	3.0	3.2	3.8	3.2	3.0	3.2	3.0
Oke11															
n	100	80	90	88	45	93	100	100	99	84	89	100	85	97	39
H_e	0.56	0.59	0.61	0.53	0.69	0.54	0.54	0.56	0.61	0.60	0.60	0.58	0.59	0.60	0.63
H_o	0.58	0.58	0.62	0.58	0.69	0.56	0.59	0.61	0.57	**0.49**	0.60	0.54	0.59	0.59	0.64
A_r	4.7	4.7	4.9	4.4	5.1	4.5	4.5	4.9	4.4	4.7	4.2	4.9	4.1	4.5	4.6
Ots103															
n	99	85	99	87	45	89	100	100	100	85	88	100	98	99	40
H_e	0.95	0.93	0.95	0.94	0.93	0.95	0.93	0.94	0.94	0.93	0.94	0.94	0.93	0.91	0.94
H_o	0.93	0.93	0.94	0.94	0.96	0.94	**0.88**	0.96	0.90	**0.86**	0.93	0.90	0.91	0.89	**0.85**
A_r	17.0	15.5	17.5	16.8	15.8	17.4	15.9	17.0	15.3	15.5	16.0	16.8	14.8	14.2	15.5
Oki1L															
n	100	89	100	87	46	93	100	100	100	85	90	100	98	98	40
H_e	0.43	0.38	0.41	0.46	0.40	0.43	0.39	0.41	0.45	0.48	0.52	0.41	0.37	0.47	0.52
H_o	0.41	0.42	0.49	0.47	0.37	0.43	0.37	0.44	0.45	0.40	0.50	0.39	0.35	0.48	0.58
A_r	3.0	2.3	2.4	2.5	2.3	2.5	2.8	2.7	2.2	2.8	2.5	2.4	2.2	2.7	2.4
Oki1U															
n	98	86	100	87	43	80	97	99	100	82	88	100	95	91	36
H_e	0.91	0.91	0.89	0.90	0.92	0.91	0.91	0.92	0.83	0.88	0.87	0.91	0.84	0.85	0.83
H_o	0.90	0.94	0.88	0.89	0.95	0.90	0.91	0.95	0.89	0.93	0.90	0.87	0.87	0.82	0.83
A_r	11.8	11.2	11.3	11.5	12.9	12.0	11.6	12.2	9.4	11.1	10.7	11.7	10.4	10.3	9.9
Oki100															
n	100	68	100	87	45	93	99	98	97	74	91	100	95	94	38
H_e	0.89	0.90	0.90	0.91	0.89	0.89	0.89	0.90	0.83	0.81	0.81	0.87	0.80	0.83	0.83
H_o	0.91	0.84	0.90	0.92	0.96	0.88	0.88	0.92	0.82	0.76	0.75	0.81	0.83	0.83	0.92
A_r	12.5	12.2	12.7	13.4	11.6	13.2	12.7	12.7	10.2	11.0	10.0	11.5	10.4	11.8	10.5

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Table A2 (*concluded*).

	Population														
Locus	YS1	YS2	YS3	YS4	YS5	YS6	YS7	YS8	YS9	YS10	YS11	YS12	YS13	YS14	YS15
Oki2															
n	100	85	97	88	44	91	99	96	100	77	89	100	98	100	37
H_e	0.89	0.89	0.88	0.90	0.88	0.89	0.90	0.90	0.81	0.86	0.85	0.88	0.83	0.83	0.83
H_o	0.93	0.86	0.90	0.93	0.84	0.90	0.87	0.89	0.79	0.84	0.79	0.93	0.82	0.81	0.89
A_r	10.0	9.4	9.6	10.5	9.4	10.1	10.4	10.7	8.4	9.0	9.2	9.3	8.9	8.6	8.5
Omy101															
n	92	53	100	88	43	93	100	99	100	85	90	100	93	97	39
H_e	0.92	0.93	0.93	0.93	0.94	0.91	0.94	0.93	0.90	0.90	0.90	0.91	0.90	0.89	0.88
H_o	0.91	0.92	0.91	0.92	0.98	0.97	0.92	0.95	0.93	0.86	0.88	0.92	0.92	0.91	0.92
A_r	14.6	14.4	14.5	14.9	15.6	13.9	15.4	15.0	12.7	13.8	11.9	13.9	12.5	12.5	11.8
One101															
n	100	85	100	89	45	92	97	95	98	83	90	100	94	98	37
H_e	0.90	0.89	0.89	0.90	0.90	0.90	0.90	0.90	0.88	0.88	0.87	0.90	0.82	0.83	0.88
H_o	0.89	0.88	0.88	0.88	0.89	0.85	0.95	0.88	0.83	**0.81**	0.88	0.92	0.81	0.85	0.89
A_r	13.8	13.1	12.5	13.7	12.9	13.4	12.9	13.1	12.5	12.2	11.4	13.1	9.3	10.2	10.5
One102															
n	100	88	99	86	44	92	100	99	99	84	91	100	96	99	39
H_e	0.91	0.91	0.90	0.91	0.91	0.91	0.91	0.91	0.90	0.90	0.89	0.90	0.90	0.90	0.90
H_o	**0.84**	0.88	0.94	0.94	0.95	0.92	**0.80***	0.92	0.87	0.89	0.91	0.90	0.89	0.92	0.92
A_r	11.4	11.2	10.7	11.2	11.6	11.0	11.1	11.3	11.0	10.7	10.2	10.9	10.9	11.1	11.0
One104															
n	98	84	99	88	41	90	99	100	97	72	91	100	95	100	27
H_e	0.93	0.93	0.92	0.93	0.90	0.94	0.94	0.93	0.91	0.89	0.90	0.93	0.90	0.91	0.93
H_o	0.96	0.94	0.93	0.91	0.83	0.93	0.94	0.95	0.93	0.92	0.89	0.91	0.87	0.92	0.89
A_r	14.8	14.8	14.3	14.8	12.9	15.7	15.5	14.7	14.0	13.0	12.8	15.2	12.9	13.1	14.0
One114															
n	57	80	100	85	43	93	100	99	98	73	91	100	98	95	35
H_e	0.92	0.92	0.91	0.93	0.93	0.93	0.92	0.92	0.89	0.90	0.89	0.92	0.90	0.90	0.91
H_o	0.93	0.90	0.88	0.98	1.00	0.96	0.91	0.94	0.90	0.88	0.90	0.91	0.90	0.96	0.91
A_r	14.2	13.6	12.7	14.1	14.9	14.0	13.1	13.5	11.1	12.0	11.4	13.6	12.0	11.8	11.8
Otsl															
n	99	88	100	89	44	92	99	99	92	84	91	100	96	100	39
H_e	0.77	0.78	0.72	0.75	0.66	0.72	0.79	0.72	0.72	0.81	0.73	0.73	0.67	0.70	0.72
H_o	0.75	0.72	0.70	0.79	0.68	0.67	0.78	0.71	0.66	**0.67***	0.80	0.78	0.74	0.72	0.79
A_r	7.9	8.6	6.6	7.5	6.6	6.3	8.5	6.1	8.9	7.8	5.7	6.8	6.5	6.5	5.6
Otsg68															
n	100	84	100	88	45	93	100	100	100	78	90	100	94	96	40
H_e	0.94	0.94	0.93	0.94	0.93	0.94	0.94	0.94	0.92	0.92	0.92	0.95	0.91	0.91	0.93
H_o	**0.87***	0.89	0.97	0.94	0.91	0.96	0.91	0.94	0.89	0.90	0.93	0.93	0.91	0.92	0.98
A_r	16.8	16.1	15.4	15.7	15.2	16.2	15.8	15.8	14.0	14.2	14.4	17.6	13.0	13.6	14.1
Ssa419															
n	100	82	100	79	43	91	96	97	98	51	91	100	90	97	37
H_e	0.86	0.82	0.88	0.86	0.84	0.86	0.83	0.87	0.88	0.85	0.88	0.84	0.85	0.84	0.85
H_o	0.89	0.88	0.91	0.92	0.86	0.87	0.83	0.90	0.89	0.82	0.92	0.84	0.89	0.87	0.86
A_r	9.7	8.3	10.1	9.2	8.9	9.7	8.8	10.0	9.5	8.8	9.6	9.2	8.9	9.0	8.1
Average															
n	97	84	97	87	43	90	99	99	99	80	90	100	94	97	37
H_e	0.68	0.68	0.69	0.69	0.68	0.68	0.68	0.69	0.67	0.67	0.68	0.68	0.66	0.66	0.68
H_o	0.68	0.67	0.69	0.69	0.69	0.68	0.67	0.70	0.67	0.64	0.68	0.68	0.66	0.67	0.70
A_r	9.0	8.6	8.6	8.9	8.7	8.8	8.8	8.9	8.0	8.2	7.8	8.7	7.6	7.8	7.7

Note: Sample abbreviations are as indicated in Table 1. A bold value indicates that the sample–locus does not conform to Hardy–Weinberg expectation ($p < 0.05$). An asterisk (*) indicates that the p value was judged significant when the α level (0.05) was adjusted for simultaneous tests (see text). Allelic richness (A_r) estimates are based on a minimum sample size of 27 diploid individuals. n, sample size; H_e, expected heterozygosity; H_o, observed heterozygosity.

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Table A3. Genetic diversity at 20 microsatellite loci in fall-run chum salmon (*Oncorhynchus keta*) population samples from the Yukon River (YF).

	Population													
Locus	YF1	YF2	YF3	YF4	YF5	YF6	YF7	YF8	YF9	YF10	YF11	YF12	YF13	YF14
Oki23														
n	70	100	100	100	100	100	94	75	90	88	99	63	100	95
H_e	0.39	0.43	0.38	0.48	0.50	0.56	0.44	0.48	0.49	0.47	0.42	0.46	0.42	0.39
H_o	0.36	**0.36**	0.41	0.50	0.57	0.57	0.49	0.50	0.59	0.47	0.48	0.47	0.41	0.37
A_r	2.5	2.7	2.7	3.0	2.9	3.0	2.9	2.9	2.9	2.9	2.9	2.9	2.6	3.0
Oke8														
n	70	100	100	100	100	100	94	75	87	87	99	63	100	97
H_e	0.01	0.08	0.03	0.01	0.06	0.06	0.01	0.01	0.01	0.06	0.03	0.01	0.05	0.03
H_o	0.01	0.06	0.03	0.01	0.06	0.06	0.01	0.01	0.01	0.06	0.03	0.01	0.05	0.03
A_r	1.2	1.8	1.4	1.2	1.7	1.7	1.2	1.2	1.2	1.6	1.5	1.2	1.6	1.4
Oke3														
n	70	100	100	100	100	100	92	75	77	87	99	61	96	97
H_e	0.57	0.61	0.57	0.61	0.62	0.62	0.62	0.67	0.64	0.65	0.67	0.51	0.52	0.64
H_o	0.56	0.63	**0.44***	0.64	0.67	0.71	0.56	0.68	0.60	0.64	0.67	0.45	0.49	0.62
A_r	4.4	4.2	3.6	3.8	3.8	3.8	4.0	4.0	3.9	3.9	3.9	2.7	2.8	3.8
Oke4														
n	69	100	100	100	98	100	92	72	55	87	99	52	87	97
H_e	0.03	0.02	0.06	0.14	0.15	0.16	0.20	0.16	0.16	0.05	0.13	0.12	0.08	0.32
H_o	0.03	0.02	0.06	0.15	0.15	0.16	**0.16**	0.17	0.17	**0.02**	0.14	0.13	0.08	0.30
A_r	1.4	1.3	1.7	2.2	2.4	2.5	2.4	2.4	2.3	1.6	2.1	2.0	1.8	2.6
Ots2.1L														
n	70	100	100	100	94	100	91	73	88	88	99	64	98	97
H_e	0.04	0.12	0.09	0.12	0.21	0.17	0.14	0.20	0.21	0.23	0.13	0.26	0.18	0.04
H_o	0.04	0.13	0.09	0.13	0.21	0.18	0.13	0.20	0.23	0.19	0.14	0.24	0.14	0.04
A_r	1.5	2.0	1.8	1.9	2.0	2.0	1.9	2.0	2.0	2.0	1.9	2.0	2.0	1.5
Ots2.1U														
n	70	100	100	100	96	100	91	72	87	87	99	64	98	97
H_e	0.57	0.58	0.61	0.62	0.63	0.56	0.61	0.60	0.57	0.58	0.57	0.54	0.46	0.60
H_o	0.67	0.59	0.59	0.63	0.69	0.58	0.65	**0.51**	0.60	0.61	0.57	0.59	0.47	0.60
A_r	3.2	3.2	3.3	3.4	3.2	3.0	3.7	3.2	3.0	3.0	3.0	3.0	3.0	3.2
Oke11														
n	70	100	100	100	100	100	91	75	89	90	99	65	98	95
H_e	0.57	0.57	0.57	0.53	0.58	0.55	0.55	0.58	0.58	0.53	0.58	0.60	0.60	0.57
H_o	0.51	0.57	0.59	0.56	0.59	0.58	0.49	0.56	0.55	0.51	0.61	0.54	0.57	0.55
A_r	4.4	4.6	4.3	4.2	4.3	3.8	4.0	4.5	4.4	4.3	4.6	3.7	3.0	4.5
Ots103														
n	70	100	100	100	100	100	94	75	89	87	99	64	99	96
H_e	0.93	0.92	0.93	0.94	0.94	0.94	0.94	0.93	0.94	0.94	0.94	0.92	0.92	0.91
H_o	0.93	0.89	0.93	0.92	0.96	1.00	0.91	0.93	0.92	**0.88**	0.94	0.91	0.94	0.89
A_r	14.6	14.0	14.7	16.1	15.7	15.6	15.7	15.0	15.5	15.4	15.9	13.9	13.1	13.1
Oki1L														
n	70	100	100	100	100	100	94	75	91	89	99	65	99	97
H_e	0.45	0.40	0.46	0.52	0.51	0.50	0.49	0.50	0.50	0.50	0.51	0.50	0.50	0.49
H_o	0.49	**0.32**	0.51	0.56	0.50	0.49	0.51	0.56	0.55	0.45	0.47	0.48	0.68	0.44
A_r	2.2	2.3	2.2	2.4	2.2	2.2	2.3	2.0	2.2	2.0	2.2	2.0	2.0	2.0
Oki1U														
n	68	100	100	94	100	100	92	73	58	86	99	57	86	94
H_e	0.83	0.86	0.83	0.84	0.81	0.81	0.84	0.85	0.86	0.83	0.86	0.85	0.85	0.88
H_o	0.79	0.83	0.80	0.88	**0.70***	0.77	0.80	0.88	0.88	0.76	0.81	0.79	0.81	0.91
A_r	9.3	11.0	9.8	10.3	9.4	9.0	10.4	10.5	9.5	8.9	10.2	8.5	8.0	9.8
Oki100														
n	66	100	100	98	97	100	92	16	89	89	99	55	95	81
H_e	0.85	0.85	0.80	0.75	0.84	0.84	0.79	0.85	0.88	0.82	0.85	0.70	0.69	0.86
H_o	0.80	0.86	0.79	0.73	0.84	0.79	0.77	0.84	0.88	0.87	0.81	0.72	0.75	0.93
A_r	10.4	10.0	8.5	8.4	10.3	9.4	8.9	10.1	10.0	9.5	9.8	7.4	7.0	9.6

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Table A3 (*concluded*).

	Population													
Locus	YF1	YF2	YF3	YF4	YF5	YF6	YF7	YF8	YF9	YF10	YF11	YF12	YF13	YF14
Oki2														
n	69	100	100	91	90	100	90	42	86	84	99	60	94	92
H_e	0.70	0.82	0.80	0.74	0.70	0.77	0.72	0.64	0.56	0.68	0.68	0.72	0.73	0.72
H_o	0.70	0.80	0.84	0.76	0.69	0.88	0.69	0.66	0.55	0.69	0.63	0.76	0.77	0.68
A_r	7.1	8.3	8.1	8.4	8.7	7.4	8.3	8.0	6.9	8.9	8.3	6.9	6.4	6.3
Omy101														
n	47	100	100	69	99	100	70	25	86	58	99	57	95	86
H_e	0.91	0.91	0.93	0.91	0.90	0.92	0.91	0.91	0.92	0.93	0.92	0.85	0.82	0.91
H_o	0.85	0.90	0.93	0.87	0.90	0.92	0.92	0.89	0.96	0.93	0.91	0.82	0.79	0.91
A_r	12.6	12.7	14.0	12.8	12.6	13.8	13.5	13.1	12.2	13.5	13.6	10.6	11.0	12.5
One101														
n	70	100	98	98	99	100	91	69	60	52	99	52	95	82
H_e	0.85	0.85	0.83	0.87	0.84	0.82	0.87	0.83	0.85	0.83	0.87	0.88	0.90	0.70
H_o	0.83	0.79	0.82	**0.79**	0.85	0.81	0.83	0.82	0.86	0.85	0.85	0.89	0.87	0.70
A_r	8.7	9.8	9.0	11.2	10.3	8.8	10.6	10.3	9.9	10.6	11.4	10.6	11.0	7.2
One102														
n	69	100	100	98	100	100	76	63	92	90	99	63	96	95
H_e	0.90	0.89	0.90	0.90	0.90	0.90	0.89	0.91	0.89	0.90	0.89	0.89	0.86	0.86
H_o	0.93	0.84	0.89	**0.73***	0.91	**0.81**	0.90	**0.74***	0.83	0.86	**0.83**	0.85	0.87	0.84
A_r	10.6	9.7	10.7	10.4	10.3	10.1	10.1	11.2	9.6	10.7	10.1	10.4	10.0	8.9
One104														
n	66	100	100	92	91	100	70	70	66	75	99	59	94	71
H_e	0.89	0.85	0.86	0.93	0.91	0.90	0.92	0.91	0.91	0.94	0.91	0.90	0.88	0.85
H_o	0.91	0.88	0.86	**0.85**	0.95	0.91	0.89	0.93	0.86	0.94	0.87	0.88	0.90	0.86
A_r	11.8	11.0	10.8	14.2	13.5	13.1	13.6	14.3	12.5	14.4	13.1	11.1	10.3	11.6
One114														
n	69	100	99	98	94	100	91	28	90	89	99	58	98	96
H_e	0.87	0.87	0.82	0.90	0.90	0.90	0.88	0.89	0.86	0.88	0.88	0.85	0.83	0.85
H_o	0.90	0.88	0.89	**0.84**	0.90	0.92	0.87	0.92	0.96	0.91	0.97	0.84	0.83	0.97
A_r	10.6	11.1	10.6	11.7	11.3	11.3	10.9	10.9	8.2	10.2	9.9	8.4	7.2	8.1
Otx3														
n	69	100	100	98	98	100	94	50	90	86	99	63	98	91
H_e	0.66	0.71	0.76	0.72	0.72	0.67	0.72	0.70	0.63	0.71	0.68	0.79	0.78	0.65
H_o	0.77	0.73	0.72	**0.58***	0.70	0.70	**0.65**	0.77	0.56	0.74	0.62	0.82	0.81	**0.57**
A_r	6.5	6.3	7.9	7.3	5.7	5.5	7.4	6.2	4.3	6.2	5.0	6.7	6.0	4.6
Otsg68														
n	67	100	100	99	97	100	89	63	88	87	99	64	98	95
H_e	0.89	0.92	0.89	0.92	0.91	0.91	0.92	0.90	0.89	0.91	0.90	0.87	0.87	0.88
H_o	0.85	0.90	0.88	0.90	0.93	0.95	0.90	0.88	0.89	0.94	0.95	0.96	0.94	0.95
A_r	10.6	13.3	11.6	13.9	12.7	13.5	14.1	13.0	11.7	12.6	12.5	10.3	10.3	10.2
Ssa419														
n	63	100	99	96	84	100	87	75	82	82	99	62	96	92
H_e	0.83	0.86	0.86	0.85	0.85	0.84	0.86	0.84	0.85	0.83	0.84	0.81	0.82	0.86
H_o	0.79	**0.79**	0.93	0.96	0.89	0.91	**0.79**	0.90	0.92	0.87	0.90	0.93	0.90	0.89
A_r	8.2	8.7	8.7	8.3	8.3	8.2	8.1	7.8	7.5	7.3	7.4	7.3	6.5	7.7
Average														
n	68	100	100	97	97	100	89	62	82	83	99	61	96	92
H_e	0.64	0.66	0.65	0.66	0.67	0.67	0.67	0.67	0.66	0.66	0.66	0.65	0.64	0.65
H_o	0.64	0.64	0.65	0.65	0.68	0.69	0.65	0.67	0.67	0.66	0.66	0.65	0.65	0.65
A_r	7.1	7.4	7.3	7.8	7.6	7.4	7.7	7.6	7.0	7.5	7.5	6.6	6.3	6.6

Note: Sample abbreviations are as indicated in Table 1. A bold value indicates that the sample–locus does not conform to Hardy–Weinberg expectation ($p < 0.05$). An asterisk (*) indicates that the p value was judged significant when the α level (0.05) was adjusted for simultaneous tests (see text). Allelic richness (A_r) estimates are based on a minimum sample size of 16 diploid individuals. *n*, sample size; H_e, expected heterozygosity; H_o, observed heterozygosity.

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Assessing the importance of macroinvertebrate trophic dead ends in the lower transfer of methylmercury in littoral food webs

Fabien Cremona, Dolors Planas, and Marc Lucotte

Abstract: Total mercury and methylmercury concentrations ([THg], [MeHg]) were measured in littoral macroinvertebrates from Lake St. Pierre, Quebec, Canada. Functional groups (detritivore, grazer, edible predator, inedible predator) explained the greatest fraction of [MeHg] variation compared with time (year, month), and space (station and shore). Greatest [THg] and [MeHg] were found in inedible predators mostly from families of heteropterans and coleopterans. Detritivores and grazers exhibited the lowest Hg concentrations, while edible predators were intermediate. Inedible predators also had the highest percentage of MeHg ([MeHg]/[THg]), with some taxa close to 100%. Such high percentages are seldom observed in freshwater organisms other than piscivorous fish. MeHg burden (concentrations × biomass) in inedible predators accounted for 10% of the MeHg pool for the whole invertebrate community. These large quantities of MeHg are sequestrated in aquatic "trophic dead ends" and could partly explain the low [MeHg] measured in fish, compared with [MeHg] of macroinvertebrates from Lake St. Pierre and other freshwater ecosystems with large littoral zones. We recommend taking into account the inedible organisms in Hg cycling models to avoid a possible overestimation of the MeHg pool available to fish.

Résumé : Nous avons mesuré les concentrations en mercure total et méthylmercure ([THg] et [MeHg]) chez les macroinvertébrés littoraux du lac Saint Pierre, Québec, Canada. Le groupe fonctionnel (détritivore, brouteur, prédateur consommable, prédateur non consommable) explique la plus forte proportion de la variation de [MeHg] comparé au temps (année, mois) et à l'espace (station, rive). Les plus fortes [THg] et [MeHg] se retrouvent chez les prédateurs non consommables appartenant à des familles de coléoptères et d'hétéroptères. Les détritivores et les brouteurs montrent les plus faibles concentrations, alors que les prédateurs consommables sont intermédiaires. Les prédateurs non consommables présentent également les plus forts pourcentages de MeHg ([MeHg]/[THg]), avec certains taxons proches de 100 %. De tels pourcentages ne sont habituellement observés en eau douce que chez les poissons piscivores. La charge de MeHg (concentration × biomasse) chez les prédateurs non consommables représente 10 % du réservoir de MeHg de la communauté des macroinvertébrés. Cette quantité importante de MeHg est séquestrée dans des impasses trophiques aquatiques et pourrait expliquer partiellement les faibles [MeHg] mesurées chez les poissons comparées aux [MeHg] des macroinvertébrés du lac Saint Pierre et des autres écosystèmes d'eau douce avec des zones littorales étendues. Nous recommandons de tenir compte des organismes non consommables dans les modèles de cycle du Hg afin de ne pas surestimer les quantités de MeHg disponibles pour les poissons.

Introduction

Monomethylmercury (MeHg) is considered a global threat to human and ecosystem health because of its neurotoxicity and accumulation in food webs through biomagnification (Boening 2000). Since fish consumption is the main pathway for MeHg to enter the human body, several studies considered factors affecting MeHg concentrations ([MeHg]) in fish (MacCrimmon et al. 1983; Cabana et al. 1994; Simoneau et al. 2005). However, other components of the mercury (Hg) food web have often been overlooked. For example, benthic macroinvertebrate have received less attention than pelagic invertebrates as prey organisms for fish. The few reported data demonstrate that [MeHg] in macroinvertebrates can be very high (Tremblay et al. 1996; Hall et al. 1998; Désy et al. 2000). Since macroinvertebrates constitute an important food source for juvenile and adult fish, they play a crucial role in energy transfer in lakes (Bertolo et al. 2005). This fact should be even more important in shallow lakes with large littoral zones covered with aquatic plants, where invertebrates dwelling in macrophytes constitute a larger fraction of the prey of insectivorous and juvenile piscivorous fish and where pelagic phytoplankton productivity does not account for a large part of total productivity (Vis et al. 2007). In systems where periphyton productivity is important, Hg methylation rates may be high, thus leading to elevated [MeHg] in epiphytic biofilms (Cleckner et al. 1998). Hence, littoral invertebrates may con-

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stitute a crucial link between the Hg-methylating environment of epiphytes and top predators.

In vegetated littoral environments of lakes and lentic waters of rivers, the invertebrate fauna is unique because it is not dominated by insect larvae as in lotic environments. Instead aquatic adults of insect species, named "secondary invaders" (Hynes 1984) because of their recent terrestrial origin, constitute a non-negligible share of the invertebrate community, along with non-insect taxa like gastropods and amphipods. The majority of the imago stages of insect species living in vegetated water bodies, mostly heteropterans and coleopterans, have developed chemical defences that render them unpalatable (Eisner and Aneshansley 2000). Thus, they are resistant to predation and are seldom eaten by fish (Polhemus 1996). Though fish are able to exclude some heteropterans and coleopterans from small lakes (Bendell and McNicol 1987), it is not well known whether it is caused by predation or competitive exclusion. It has been experimentally demonstrated that largemouth bass (*Micropterus salmoides*) force fed with edible worms coated with *Dineutus hornii* (Coleoptera: Gyrinidae) abdominal gland secretion rejected the prey (Eisner and Aneshansley 2000). A decade-long field survey of the stomach contents of 18 fish species of the St. Lawrence River revealed that heteropterans and coleopterans constituted a negligible part of the fish diet (Latour et al. 1980). Large individuals of heteropterans and coleopterans are not only weakly affected by fish predation but can even become top predators in fishless lakes (Runck and Blinn 1994) and turn out to be pests in fish nurseries (Wilson 1958; Le Louarn and Clourec 1997). Because of their trophic position and low predation pressure, inedible predatory insects are more susceptible to MeHg accumulation than edible ones. They also have the potential to live longer than edible predators and hence accumulate even greater [MeHg]. The MeHg pool these invertebrates represent would thus be unavailable to aquatic predators, including fish.

The goal of this study was to assess the contribution of inedible predatory insects to the MeHg pool in the macroinvertebrate littoral communities in a large fluvial lake, Lake St. Pierre, which receives high Hg loadings from its tributaries (Quémerais et al. 1999) and which hosts extensive macrophyte beds. We tested the following hypotheses: (*i*) variations in [MeHg] in macroinvertebrates are better explained by trophic factors than by spatial differences in Hg loadings; (*ii*) the amount of Hg that is sequestrated in inedible predators is equal or greater to that represented by edible predators.

Materials and methods

Study site

Lake St. Pierre is a large fluvial lake of the St. Lawrence River (46°02′–05′N, 72°39′W) southern Quebec, Canada. Its macrophyte beds represent one-fifth and three-quarters of all St. Lawrence River wetlands and marshes, respectively (Langlois et al. 1992). These wetlands are highly productive (Tessier et al. 1984), with macrophytes and attached epiphytes contributing up to 70% of lake primary production (Vis et al. 2007). There are three markedly distinct water masses flowing in Lake St. Pierre: brown waters, rich in dissolved organic carbon (DOC), from the Ottawa River inflow and other Canadian Shield tributaries arriving on the northern section of the lake (Vis et al. 2003); clear waters from Lake Ontario flow in the central channel; and tributaries draining extensively farmed lands bring turbid waters from the Appalachian region on the southern section of Lake St. Pierre (Vis et al. 2003). The central channel is part of the St. Lawrence Seaway; it is artificially dredged and prevents the mixing of the north and south water masses. High Hg loadings are associated with terrigenous organic matter in the south shore tributaries (Quémerais et al. 1999), in contrast with lower Hg loadings brought by the north shore tributaries that have more forested watersheds. Hg loads from the southern main tributaries (Richelieu, Saint-François, and Yamaska rivers) have been estimated between >120 and 733 mol Hg·year^{-1} (Quémerais et al. 1999). Tributaries from the north shore (Maskinongé, Rivière-du-Loup, and Yamachiche rivers) discharge comparatively little Hg: 4 mol Hg·year^{-1}. Dissolved THg concentrations are low in Lake St. Pierre, averaging 1.50 ng·L^{-1} in the south shore tributaries and 1.14 ng·L^{-1} elsewhere (S. Caron and M. Lucotte, Université du Québec à Montréal, unpublished data). MeHg concentrations are generally below 1 ng·L^{-1} at all stations (S. Caron and M. Lucotte, Université du Québec à Montréal, unpublished data). Hg bound to suspended particulate matter usually represents 40% of total Hg present in the water column.

Collecting and sorting invertebrates

Sampling was conducted monthly from July to September 2003 and from May to September 2004 at four sites in Lake St. Pierre. Two sites were situated in the brown waters of the north shore of the lake (GIR, MAS) and two others on the turbid waters of the south shore (ADF, BSF). Invertebrates were collected in macrophyte beds, with a Plexiglas-modified (15 cm × 35 cm × 25 cm) Downing box (Downing 1984). The sampler was immersed in the water between the surface and 1.5 m deep and then slowly closed, capturing both vagile and phytophilous invertebrates. Six replicates were collected at each station in May and June in 2004 and nine replicates from July to September in 2003 and 2004. An aquatic hand net was used as a complement to catch very fast-moving insects like Dytiscidae and Gyrinidae. All bulk samples were sieved through a 500 µm net, and macroinvertebrates were separated from macrophytes by vigorous hand shaking in a plastic container filled with lake water. Macroinvertebrates were presorted to isolate predators from prey and kept in Nalgene jars filled with lake water for at least 4 h.

Macroinvertebrate identification and Hg analysis

Organisms were kept frozen at –80 °C prior to analysis. Invertebrates were identified usually to family or genus. Shells of gastropods were removed manually with stainless steel tweezers. For taxonomic identification, the following keys were used: Merrit and Cummins (1996) for insects, Clarke (1981) for gastropods, and Pennak (1953) for other macroinvertebrates. We grouped the samples into four functional groups: grazers (including all invertebrates feeding on live plants), detritivores (invertebrates feeding on dead plants and animals), edible predators or parasites (called

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edible predators hereafter), and inedible predators (insects seldom eaten by fish because of their chemical defenses, Eisner and Meinwald 1966). The following taxa were included in the latter group: Heteroptera: Belostomatidae (Lokensgard et al. 1993), Gerridae and Mesoveliidae (Bronmark et al. 1984), Notonectidae (Pattenden and Staddon 1968), Pleidae (Maschwitz 1967), Coleoptera: Dytiscidae (Swevers et al. 1991), and Gyrinidae (Eisner and Aneshansley 2000). Though they belong to heteropterans, Corixidae (water boatmen) were not included in the inedible predators group because they are heavily preyed upon by fish and other predators (Polhemus 1996). Hydracarina (water mites) might also be unpalatable to fish (Kerfoot 1982), but a more recent review only found anecdotal evidence of mite rejection by fish predators (Zhang 1998), so for the purpose of this study they were considered as edible.

All instruments used for sample processing were rinsed once with 10% HCl and twice with nanopure water. Invertebrates were freeze-dried for 48 h, and to avoid manipulation and possible contamination, ground with a glass rod directly in the vial. Subsamples were then weighed on an electrobalance (AT201 Mettler Toledo, Canada). Each individual taxon was kept in a separate vial. Because the mean weight of our samples was often below 5 mg dry weight (DW), we used THg and MeHg analysis methods described by Pichet et al. (1999). These methods allow for the processing of small samples, as little as <1 mg DW. Total Hg concentrations ([THg]) were obtained with cold vapor fluorescence atomic spectrometry (Bloom 1989) with a detection limit of 1 ng·g^{-1}. The sole difference with Bloom method was that Hg was not preconcentrated in a gold column but was injected directly. Reproducibility was verified with the National Research Council of Canada standard TORT-2 (lobster hepatopancreas). The measured concentrations of TORT-2 were always within the certified value of 270 ± 60 ng·g^{-1} DW (n = 27). For MeHg analyses, a saponification technique with a detection limit of 0.6 pg of MeHg, modified from Bloom (1989) by Pichet et al. (1999) was used. Briefly, the digestion of 0.5–5 mg DW invertebrate was performed in 0.5 mL of a KOH–MeOH (1 g·4 mL^{-1}) solution during 8 h at 68 °C. MeHg was then converted to methylethyl Hg (MeEtHg) with sodium tetracthylborate in a buffered solution at pH 4.5. MeEtHg was then trapped in a column, separated by gas chromatography, and quantified using CVAFS. The reproducibility of the method was verified by analyzing two National Research Council standard reference materials, DORM-1 (dogfish muscle) and TORT-2, that yielded a mean value ± standard deviation (SD) of 742 ± 93 (n = 37) and 157 ± 17 ng·g^{-1} DW (n = 11), respectively, as compared with the certified values of 731 ± 60 ng·g^{-1} DW and 152 ± 13 ng·g^{-1} DW, repsectively. Samples that lead to proportions of MeHg above 115% of THg were discarded.

Data treatment

Values of [MeHg] were log-transformed prior to statistical analysis. We used factorial test effect models (JMP 5.1, SAS Institute Inc., Cary, North Carolina) to take into account the influence of temporal (2 years and 5 months), spatial (4 stations, 2 shores), and trophic level (4 functional groups) categorical variables on [MeHg] (SAS Institute Inc. 1991; Uryu et al. 2001). For each statistical level, comparisons between groups based on adjusted values (least-squared means) were performed with analysis of variance (ANOVA) and Tukey–Kramer honestly significant differences (HSD).

For each taxon (t) and each sample, we calculated MeHg burden, which represents a quantitative method to estimate the MeHg pool per functional group, in addition to measurements of [MeHg]. Because an aquatic hand net is not a quantitative sampler, only samples collected with a Downing box were considered for burden calculation.

We calculated MeHg burden with the following equation:

$$(1)\quad \text{MeHg burden}_t = [\text{MeHg}]_t \times W_t$$

where MeHg burden$_t$ is in ng; [MeHg]$_t$ is in ng·g^{-1} DW; and W_t is in ng DW for each taxon of invertebrates. Then, the MeHg burdens of each taxon (t_1, t_2, …, t_n) within a given functional group (a) at a given station (nine Downing boxes) and at each month were added:

$$(2)\quad \text{MeHg burden}_a = \text{MeHg burden}_{t_1,a} + \text{MeHg burden}_{t_2,a} + \ldots + \text{MeHg burden}_{t_n,a}$$

The MeHg burden share of a functional group (a) among four functional groups (a,b,c,d) is calculated with the following equation:

$$(3)\quad \%\text{share}_a = [\text{MeHg burden}_a/(\text{MeHg burden}_a + \text{MeHg burden}_b + \text{MeHg burden}_c + \text{MeHg burden}_d)] \times 100$$

In addition, we also calculated the MeHg burdens per individual (i) of each taxon to have an estimated amount of MeHg available per prey item of fish:

$$(4)\quad \text{MeHg burden}_i = \text{MeHg burden}_t/n_i$$

where n_i is the number of individuals within a sample of a taxon t.

Results

[THg] and [MeHg]

In Lake St. Pierre, macroinvertebrate [THg] ranged from a mean <50 ng Hg·g^{-1} DW in trichopteran families to a mean >250 ng Hg·g^{-1} in heteropterans and predatory coleopterans (Table 1). Simuliidae larvae (Diptera) had the lowest concentrations (30 ng·g^{-1} DW), while *Ranatra* sp. (Heteroptera: Nepidae (i.e., scorpion bugs)) was the taxa with the greatest [THg] (406 ng·g^{-1} DW). Trends in [MeHg] were similar to those observed in [THg]. Mean [MeHg] ranged from 11 ng·g^{-1} DW in *Odontomyia* sp. (Diptera: Stratiomyidae) to 378 ng·g^{-1} DW in *Ranatra*. On a functional group basis, the most elevated [THg] were found in inedible predators, grazers had the lowest [THg], and detritivores and edible predators [THg] were situated between these two groups (Fig. 1). As for [MeHg], levels were greatest in inedible predators, followed by predators, detritivores, and finally, grazers, which again exhibited the lowest concentrations. Overall the mean proportions of MeHg to THg ([MeHg]/[THg]) values were high, above 50% MeHg, even in primary consumers. [MeHg]/[THg], respectively, ranged from 61% ± 1% to 69% ± 4% in grazers

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Table 1. Compilation of the mean [MeHg] and [THg] (ng Hg·g^{-1} dry weight (DW) ± standard error (SE)) in invertebrates from Lake St. Pierre sampled in 2003 and 2004.

Taxon	Functional group[a]	[THg]	*n*	[MeHg]	*n*
Annelida					
Glossiphonidae	EP	91±11.91	23	41±17.56	6
Mollusca					
Prosobranchia	G	85±7.5	58	40±6.27	47
Pulmonata	G	81±5.44	110	37±4.96	75
Arachnidia					
Araneae	EP	282	1	—	—
Hydracarina	EP	134±13.46	18	55±30.46	2
Crustacea					
Gammarus fasciatus	G	60±5.77	98	45±5.25	67
Hyalella azteca	G	49±18.06	10	38±13.6	10
Asellus sp.	D	119±11.42	25	67±12.97	11
Insecta					
Ephemeroptera					
Baetidae	D	76±13.12	19	79±19.23	5
Heptageniidae	G	134	1	—	—
Odonata					
Coenagrion sp.	EP	120±7.9	52	110±9.38	21
Libellula sp.	EP	85±28.60	2	—	—
Aeschnidae	EP	85.5±23.99	4	107.5±52.5	2
Heteroptera					
Belostoma sp.	IP	143±23.35	6	121±24.83	3
Callicorixa sp.	EP	113±8.62	14	99±9.86	19
Gerris sp.	IP	176	2	—	—
Ranatra sp.	IP	406	1	378	1
Notonecta sp.	IP	236±20.19	6	242±16.25	7
Neoplea sp.	IP	162±11.91	23	150±11.93	13
Mesoveliidae	IP	159±32.44	3	163±30.46	2
Trichoptera					
Hydroptilidae	G	63±21.23	2	—	—
Leptoceridae	D	68±20.18	8	37±19.36	6
Limnephilidae	D	37±32.44	3	—	—
Phryganeidae	D	33	1	—	—
Lepidoptera					
Pyralidae	G	46±25.55	5	—	—
Coleoptera[b]					
Dytiscidae (A)	IP	220±32.98	3	177±24.83	3
Dytiscidae (L)	IP	195±28.56	4	—	—
Gyrinidae (A)	IP	155±21.59	3	39	1
Gyrinidae (L)	IP	212±32.98	4	148	1
Curculionidae	G	82	1	—	—
Haliplidae (A)	G	76	1	—	—
Hydrophilidae (L)	EP	79	1	—	—
Diptera					
Odontomyia sp.	D	79±32.98	3	11	1
Chironominae	D	81±8.81	42	61±11.10	15
Orthocladiinae	G	73±9.52	36	40±9.17	22
Tanypodinae	EP	36	1	—	—
Sciomyzidae	EP	113	1	—	—
Simuliidae	D	30±32.98	3	33	1

Note: —, no data available.

[a]D, detritivore; G, grazer; IP, inedible predator; EP, edible predator.

[b]A, adult; L, larvae.

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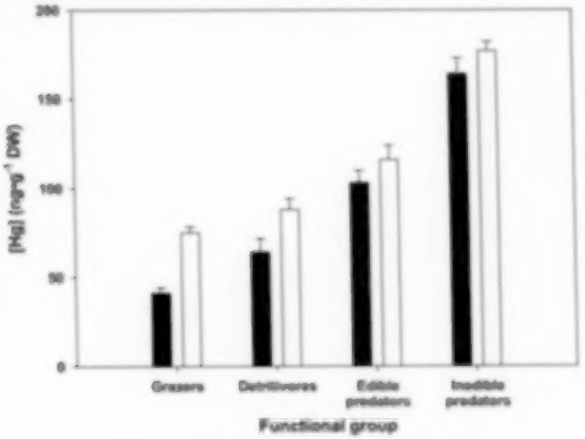
Fig. 1. Mean MeHg (solid columns) and THg (open columns) concentrations (ng·g^{-1} dry weight (DW) + standard error (SE)) of the four macroinvertebrate functional groups sampled in Lake St. Pierre.



and detritivores and from 80% ± 3% to 90% ± 4% in edible and inedible predators.

The test effect models 1 and 2 were both designed with three categorical variables (Table 2). All variables but year were highly significant. Model 1 explained slightly more of the variance of the macroinvertebrates [MeHg] than model 2 (r^2 = 0.15 compared with r^2 = 0.11, respectively). In models 3 and 4, functional group was added to models 1 and 2 as a categorical variable. Functional group was very highly significant ($p < 0.0001$) for both models and accounted for a much larger share of the variation (r^2 = 0.47) than the other variables. Additionally, the mean square of functional group was one order of magnitude greater than the mean squares of the other significant variables combined (month for models 3 and 4 and shore for model 4; Table 2). Comparisons of [MeHg] among functional groups showed that inedible predators had significantly greater [MeHg] than all the other functional groups, including edible predators and detritivores, while grazers had the lowest [MeHg] (Tukey–Kramer HSD, $p < 0.05$). [MeHg] of invertebrates from the south shore of the lake were greater than that from the north shore (ANOVA, $p < 0.05$), consistent with the reported larger Hg loadings to the southern section. Temporal differences between years were insignificant, but the differences among sampled months were highly significant. Indeed, invertebrates collected in June exhibited greater [MeHg] than those collected in the other months (Tukey–Kramer HSD, $p < 0.05$). Three distinct cases of [MeHg] monthly variations were observed among the main taxa collected in Lake St. Pierre (Fig. 2). The first case was a steady increase of [MeHg] during the season (Zygoptera). The second case was an acute drop of [MeHg] in July followed by a modest increase or decrease thereafter (Corixidae, *Neoplea*, Pulmonata). In the third case, there were nearly constant [MeHg] over the sampling season (*Gammarus*).

MeHg burden

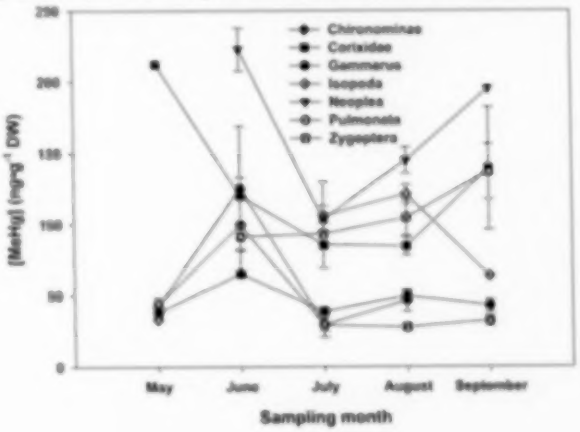
Individual transfers of MeHg in food webs where inedible predators are present are summarized (Fig. 3), with an example of a hypothetical littoral aquatic food web comprising

Table 2. Test effect model of log[MeHg] (in ng·g^{-1} dry weight (DW)) in invertebrates with selected categorical explanatory variables.

	Sum of squares	df	Mean square	*F* ratio	*p*
Model 1 (r^2 = 0.15)					
Year	0.08	1	0.08	0.15	0.69
Month	15.21	4	3.80	7.35	0.0001
Station	15.12	3	5.04	9.74	<0.0001
Model 2 (r^2 = 0.11)					
Year	0.63	1	0.63	1.16	0.28
Month	15.70	4	3.92	7.26	<0.0001
Shore	6.04	1	6.04	11.18	0.0009
Model 3 (r^2 = 0.47)					
Year	0.60	1	0.60	1.88	0.17
Month	14.85	4	3.71	11.46	<0.0001
Station	2.06	3	0.68	2.12	0.09
Functional group	68.72	3	22.90	70.71	<0.0001
Model 4 (r^2 = 0.47)					
Year	0.70	1	0.70	2.18	0.14
Month	15.21	4	3.80	11.77	<0.0001
Shore	1.72	1	1.72	5.32	0.02
Functional group	77.45	3	25.82	79.91	<0.0001

Note: Years sampled were 2003 and 2004. Months were May, June, July, August, and September. Sampling stations were ADF, BSF, GIR, MAS (see Materials and methods for a description). Shores were either the north or south end of the lake. Functional groups were detritivore, grazer, edible predator, and inedible predator.

Fig. 2. Monthly means (± standard error (SE)) of macroinvertebrate MeHg concentrations for the 2 years of sampling. Only the dominant taxa found at least in four out of five samples are shown. Functional groups are as follows: diamonds, detritivores; circles, grazers; squares, edible predators; and triangles, inedible predators.



three trophic levels. When expressed by the relative functional group's contribution by station and month of sampling, MeHg burden varied between 0 and 59 ng MeHg DW (Table 3). Grazers had the greatest mean MeHg burden (71% ± 6%), followed by predators (10% ± 3%), inedible

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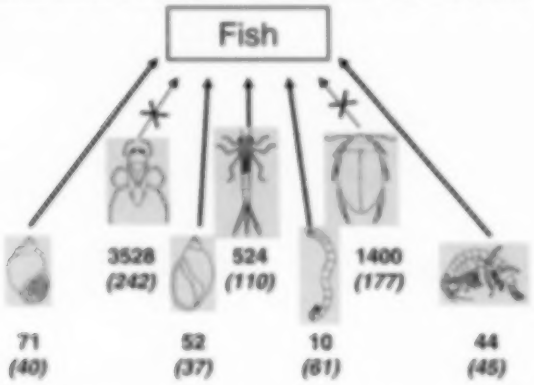
Fig. 3. Schematic representation of individual MeHg burdens (10^{-3} ng Hg) and [MeHg] (ng·g^{-1} dry weight (DW); in parentheses) in littoral macroinvertebrate potential prey to fish. Lower row represents macroinvertebrate primary consumers; middle row represents macroinvertebrate secondary consumers. Crossed lines represent inedible organisms that are avoided by fish. Drawings represent from left to right: (*i*) lower row: Bithyniidae (Prosobranchia), Physidae (Pulmonata), Chironominae (Diptera), and Gammaridae (Amphipoda); (*ii*) middle row: Notonectidae (Heteroptera), Coenagrionidae (Odonata), and Dytiscidae (Coleoptera). Macroinvertebrate drawings are modified from Bouchard (2004).



predators (10% ± 4%), and detritivores (9% ± 4%). If only stations and months with a presence of inedible predators were considered, the relative mean MeHg burdens of the functional groups were 36% ± 12% for grazers, 36% ± 10% for inedible predators, 16% ± 6% for predators, and 12% ± 7% for detritivores.

Discussion

Variations of [THg], [MeHg], and MeHg burdens

Functional group was the most important variable explaining differences in [MeHg] in macroinvertebrates, despite the fact that Hg loads are several orders of magnitude greater in the southern section of Lake St. Pierre than in the northern section (Québmerais et al. 1999) and that dissolved THg concentrations were 25% greater in the south shore tributaries compared with the rest of the lake (S. Caron and M. Lucotte, Université du Québec à Montréal, unpublished data). It has been observed that Hg loads from tributaries may not mirror [Hg] in sediments or in water. Indeed, the spring ice melt and the shallowness of the lake might be adverse to Hg retention because sediments are easily resuspended during high water episodes and then flushed downstream. Jackson (1993) hypothesized that the inorganic Hg received by a system is not enough to explain MeHg bioaccumulation in the food webs. Indeed, Hg methylation rates at the base of the food web (Desrosiers et al. 2006*a*) and (or) number of trophic levels (Cabana et al. 1994) appear as the most important factors in determining the pool of MeHg, especially in the case of macroinvertebrates, which rely more on epiphytes than on sediments for their organic matter source.

After functional group, the second most significant variable that contributed to differences in [MeHg] was the month at which samples were collected. Within the sampling period (May to September) of our study, covering most of the ice-free season, the invertebrates collected in the first week of June had the greatest [MeHg]. This is surprising, since in northern temperate latitudes, higher Hg methylation rates are usually measured in midsummer (Ullrich et al. 2001). Similarly, higher Hg methylation rates have been recorded between July and September in Quebec lakes (Desrosiers et al. 2006*a*). However, [MeHg] in organisms may not mirror the peak of methylation rate. Spring floods could indeed facilitate the penetration of bioavailable Hg in the food web (St. Louis et al. 1994; Desrosiers et al. 2006*b*) before favourable conditions for Hg methylation take place. Thus, more MeHg may be available for the food webs at the beginning of the ice-free season. In addition, the phenology of the insect larvae is another important feature that should be considered in monthly [MeHg] differences. Indeed, the replacement of the overwintering organisms by the newly hatched generation may explain why [Hg] in insects like Corixidae or *Neoplea* decreased from May–June to July and then increased towards the end of the summer and on the other hand why long-lived, large-bodied predators like damselflies (Zygoptera) showed a constant increase of [MeHg]. This increase could result from a longer ontogeny and the higher trophic positions of the prey eaten by the older instars of Zygoptera. On the contrary, taxa that have short-lived, overlapping generations like the primary consumer amphipods or gastropods showed modest changes in [MeHg]. But overall, in spite of differences in temporal and spatial conditions, the greatest dissimilarities of [MeHg] and MeHg burdens took place among functional groups.

In Lake St. Pierre, [MeHg]/[THg] were always high even at the grazer trophic level (over 50%) and reached almost 100% in predators of both types (edible and inedible). Among primary consumers, the more generalist feeders such as amphipods had the highest ratios, probably because of a substantial feeding upon animal tissues (Pennak 1953; Tate and Hershey 2003). On the contrary, herbivorous taxa like snails that scrape algae had a relatively lower [MeHg]/[THg] ($\approx$50% on average). Elevated [MeHg] and [MeHg]/[THg] in macroinvertebrates living in the macrophyte beds could be linked to the high Hg methylation rates observed in Lake St. Pierre epiphytes (Planas et al. 2004). It has been hypothesized that newly methylated Hg is most rapidly transferred in the food webs (Desrosiers et al. 2006*a*).

The bottom-up increase of Hg between primary and secondary consumers is consistent with the expected biomagnification of Hg as a function of trophic level (Cabana et al. 1994), but this has been rarely demonstrated in littoral food webs (Cleckner et al. 1998; Allen et al. 2005). These findings contradict some previous studies like those of Parkman and Meili (1993) and Tremblay et al. (1996) that showed greater [THg] in detritivores than in predators and explained these discrepancies by the characteristics of the detritic material. Samples of the latter studies included a mixture of littoral- and bottom-dwelling macroinvertebrates of boreal lakes. This habitat contrasts radically with the lush macrophyte beds of Lake St. Pierre, where the community is dominated by scrapers and not detritivores. Given that detritus has a poor nutritive value, detritivores must ingest large quantities of sediment material that is rich in

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Table 3. Methylmercury (MeHg) burden of each functional group and its relative contribution to the total MeHg burden represented by nine Downing boxes (ng MeHg) for each sampling effort.

Year-month	Site	D	G	EP	IP	Total burden[a]	% D[b]	% G	% EP	% IP
2003-07	BSF	0	0	4.55	6.95	11.50	0	0	39.56	60.44
	GIR	0	20.59	0.79	0	21.38	0	96.31	3.69	0
2003-08	ADF	0	59.53	0	0	59.53	0	100	0	0
	BSF	0	1.26	6.74	12.03	20.03	0	6.29	33.65	60.05
	GIR	0	22.44	0	0	22.44	0	100	0	0
2003-09	ADF	0	6.40	0	0	6.40	0	100	0	0
	BSF	0.12	13.77	2.61	0	16.50	0.73	83.44	15.83	0
	GIR	0	28.67	0	0	28.67	0	100	0	0
	MAS	0	20.35	5.37	0	25.72	0	79.12	20.88	0
2004-05	ADF	0	0.17	0	0	0.17	0	100	0	0
	BSF	0.35	0.58	0	0	0.94	37.87	62.13	0	0
	MAS	2.91	1.86	0	2.91	7.67	37.88	24.20	0	37.92
2004-06	ADF	0	2.95	0	0	2.95	0	100	0	0
	BSF	0	3.52	0.91	0.51	4.93	0	71.27	18.38	10.35
	GIR	0.35	5.44	3.00	0	8.79	4.01	61.89	34.10	0
	MAS	13.23	3.94	0	0	17.17	77.03	22.97	0	0
2004-07	ADF	0.60	2.06	2.55	0	5.20	11.44	39.59	48.97	0
	BSF	0.05	3.24	0.22	6.13	9.65	0.56	33.55	2.30	63.59
	GIR	0.14	6.26	1.22	0	7.62	1.87	82.18	15.95	0
	MAS	0	0.65	0	0.06	0.71	0	91.36	0	8.64
2004-08	ADF	0.37	9.94	0	0	10.31	3.63	96.37	0	0
	BSF	1.93	29.34	2.54	0	33.81	5.71	86.79	7.50	0
	GIR	0.45	31.76	0	0	32.21	1.41	98.59	0	0
	MAS	0.12	2.25	0	0	2.37	4.96	95.04	0	0
2004-09	BSF	30.59	20.39	12.44	6.83	70.24	43.55	29.03	17.71	9.72
	GIR	0	2.88	0	0	2.88	0	100.0	0	0

Note: D, detritivores; G, grazers; EP, edible predators; IP, inedible predators. See Materials and methods for a description of sampling sites.

[a]Total burden = D + G + EP + IP.

[b]% D = [D / (D + G + EP + IP)] × 100. See eq. 3.

inorganic Hg. In contrast, the majority of macroinvertebrates of Lake St. Pierre feed on epiphytic algae that have a higher nutritive value than detritus and sustain Hg methylation (Planas et al. 2004).

MeHg bioaccumulation in inedible predators

Among functional groups, inedible predators had the greatest [MeHg] and [MeHg]/[THg] of all macroinvertebrates. In some taxa, [MeHg]/[THg] were close to 100%; such high ratios have only been reported so far in piscivorous fish (Bloom 1992). In Lake St. Pierre, [MeHg] of inedible predators are indeed comparable with the [Hg] of 400 mm walleye (*Sander vitreus*; Simoneau et al. 2005). Previous research conducted in two strikingly different systems, namely, the Canadian Boreal lakes (Allen et al. 2005) and the wetlands in the Everglades (Cleckner et al. 1998), have also found that Notonectidae (an inedible predator) was the invertebrate taxon most contaminated with MeHg. However, no explanation had been advanced to explain the greater [MeHg] in inedible predators. Among several factors that could clarify this question are the life span of the inedible predators and their trophic status. We can presume that organisms that receive little predation pressure are more likely to reach their maximum life expectancy and thus accumulate more Hg. Indeed, this has been shown in insects not eaten by fish because of their large size (Wong et al. 1997). However, in our case it is not only the size that causes predation avoidance but rather chemical defences of the potential prey. The high [MeHg] in some inedible macroinvertebrates could also be explained by their fluid feeding mode. For example, the heteropterans and some coleopterans are piercers–suckers that ingest only the soft tissues of their prey compared with other predators that are chewers. Heteropterans (excluding corixids) inject enzymes into the body of their prey to dissolve internal organs and suck the resulting body fluids. In our study, minute (2 mm) *Neoplea* sp. feeding mainly upon the soft parts of microinvertebrates also exhibited very high [MeHg] compared with larger-bodied Zygoptera, which usually prey on whole organisms. MeHg concentrations are generally lower in exoskeleton of organisms compared with other body parts (Boudou et al. 1991). In our samples, the [MeHg] in exuviae of macroinvertebrates (Anisoptera, Gomphidae) was 10-fold smaller than that found in whole, postmolt adult bodies (F. Cremona, Université du Québec à Montréal, unpublished data). The importance of feeding mode for [MeHg] was also observed within the same taxon between the larvae and the adults of Gyrinidae (whirligig beetles). Whirligig beetle larvae feed exclusively on body fluids of their prey and had thrice greater [MeHg] than larvae whose adult form are also

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predatory but chewers instead of fluid feeders. The fact that adult Gyrinidae are able to prey on terrestrial invertebrates falling on the water surface and thus integrate terrestrial organic matter less contaminated in MeHg could also explain their relatively low [MeHg] compared with larvae. A final explanation of high [MeHg] in fluid-feeding inedible predators is that this feeding mode allows invertebrates to handle and kill larger prey than engulfing predators and thus receive MeHg from more contaminated, larger-bodied preys. Indeed, Dytiscidae larvae or Belostomatidae are usually able to ingest prey items the same size or larger than themselves (Peckarsky 1982; Tate and Hershey 2003).

Relative MeHg burdens of functional groups and implications for MeHg transfer to fish

Woodward and Hildrew (2002) addressed the lack of a quantitative approach in food web research, and their observation can also be applied to studies on contaminant biomagnification. Thus, MeHg burdens take into account the importance (in terms of biomass) of a given trophic level in the Hg transfer to the upper trophic levels; this information cannot be obtained using solely MeHg concentrations. In Lake St. Pierre, grazers constituted four-fifths of the biomass (F. Cremona, Université du Québec à Montréal, unpublished data), but they only accounted from one-third to three-quarters of the MeHg pool, contrasting with inedible predators that had 10 times less biomass but constituted one-tenth of the MeHg pool. These trophic dead ends thus limit during their lifetime the pool of MeHg that could be transferred to fish by secondary consumers in the aquatic food web. It is not known if these insect carcasses are edible by fish, but it can be hypothesized that as soon as defensive compounds decompose, nothing would prevent these organisms from entering the food web via detritivores.

The presence of inedible predators in a food web could explain some paradoxes about Hg contamination in fish. This is the case in Lake St. Pierre where [Hg] in walleye is consistently lower than in many other Quebec lakes (Simoneau et al. 2005), while [Hg] of invertebrates is equal or greater to that measured in previous works (Tremblay et al. 1996; Cleckner et al. 1998; Allen et al. 2005). The low [Hg] in fish with respect to their prey is explained by higher fish growth rates in Lake St. Pierre compared with other lakes (Simoneau et al. 2005). However, the majority of the MeHg found in fish flesh comes from their diet (Hall et al. 1997), and thus food web structure and food chain length (Cabana et al. 1994) might also be important. Fish that feed more on littoral zone resources might have to feed on edible but lower trophic levels compared with when they feed on longer, planktonic food chains typical of the pelagic zone. The presence of trophic dead ends may thus explain lower Hg concentrations in fish from eutrophic lakes in general (Rudd and Turner 1983; Hanten et al. 1998) and in Lake St. Pierre in particular, because many eutrophic systems are shallow and usually have vegetated beds on their littoral zones, which inedible predators favour (Polhemus 1996; Bouchard 2004).

To our knowledge, this study is the first to take into account inedibility of the organisms in MeHg cycling in ecosystems. We have demonstrated that inedible consumers have the greatest MeHg concentrations and proportions in the littoral zone. We also have shown that 10% of the macroinvertebrate MeHg pool is sequestrated in inedible organisms and thus likely unavailable to fish consumers. We thus recommend a better characterization of littoral invertebrate communities to establish better predictive models of Hg cycling in aquatic food webs, especially in the littoral zone and in wetlands. Indeed, if researchers do not take into account inedibility in studies of Hg cycling in ecosystems, this could lead to an overestimation of MeHg available to fish and impair the accuracy of these models.

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Acoustically derived fine-scale behaviors of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) associated with intertidal benthic habitats in an estuary

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Abstract: Given the presumed importance of benthic and epibenthic estuarine habitats in Chinook salmon (*Oncorhynchus tshawytscha*) smolt growth and survival, resource managers would be well served by an improved understanding of how smolts use such habitats. A cabled acoustic positioning system was used to precisely track (<1 m resolution) the movement of seventeen 0-aged hatchery-reared fall Chinook smolts in a large (~4000 m^2) enclosure over a period of 10 days in Willapa Bay, Washington, USA. A hierarchical Bayesian state–space model of movement was subsequently developed to associate the behaviors of tagged salmon with characteristics of benthic habitat in the enclosure. Model results indicated that smolts had a strong preference for remaining in native eelgrass (*Zostera marina*). Conversely, no such preference existed for other structured benthic habitats such as oyster (*Crassostrea gigas*) beds, non-native eelgrass (*Zostera japonica*), and non-native smooth cordgrass (*Spartina alterniflora*). There was a positive relationship between individual survivorship in the enclosure and the strength of behavioral preference for native eelgrass, suggesting that predator avoidance may be the evolutionary mechanism driving behavioral responses of smolts to benthic habitats.

Résumé : Étant donné l'importance présumée des habitats estuariens benthiques et épibenthiques pour la croissance et la survie des saumoneaux du saumon chinook (*Oncorhynchus tshawytscha*), une meilleure compréhension de l'utilisation de ces habitats par les saumoneaux serait utile aux gestionnaires des ressources. Nous avons utilisé un système de positionnement acoustique avec câbles pour suivre avec précision (résolution de <1 m) les déplacements de 17 saumoneaux chinook d'automne de pisciculture d'âge 0 dans un grand (~4000 m^2) enclos pendant 10 jours dans la baie de Willapa, état de Washington, É.-U. Nous avons ensuite mis au point un modèle bayésien état–espace des déplacements afin d'associer les comportements des saumons marqués à des caractéristiques de l'habitat benthique dans l'enclos. Les résultats de la modélisation indiquent que les saumoneaux montrent une forte préférence pour demeurer dans les herbiers à zostères (*Zostera marina*) indigènes. À l'inverse, il n'existe pas de telle préférence pour les autres habitats benthiques structurés, les bancs d'huîtres (*Crassostrea gigas*), les herbiers de zostères (*Zostera japonica*) non indigènes et les herbiers de spartines (*Spartina alterniflora*) non indigènes. Il existe une corrélation positive entre la survie d'un individu dans l'enclos et l'intensité de sa préférence comportementale pour la zostère indigène, ce qui fait croire que l'évitement des prédateurs peut être le mécanisme évolutif qui explique les réactions comportementales des saumoneaux aux habitats benthiques.

[Traduit par la Rédaction]

Introduction

Estuarine residence is a critical life history stage for most salmonids. The interface between fresh and salt water aids in the physiological changes of smoltification (Simenstad et al. 1982; MacDonald et al. 1987; Thorpe 1994), the abundance of food in the nearshore environment allows for rapid growth (Congleton et al. 1982), and the habitat components of the estuarine environment provide ample cover from a potentially large predator base (Wood 1987). Estuaries all along the US west coast have suffered major anthropogenic impacts such as dredging and channelization, shoreline armoring, overwater structures, water quality degradation, and the introduction of invasive species (Kennedy 1982; Bottom et al. 2005; Lotze et al. 2006). These changes have undoubtedly impacted the growth and survivorship of Pacific salmon in general, and Chinook salmon (*Oncorhynchus tshawytscha*) in particular, given that the species characteristically resides in estuaries longer than other Pacific salmonids (typically around 1 month, although as long as 6 months in larger estuary systems such as Willapa Bay, Washington) (Healey 1982*b*; Simenstad et al. 1982; Thorpe 1994).

Pacific salmon stocks have endured persistent long-term declines in habitat quality and availability over the last century and in many cases steep population declines over the last few decades (Nehlsen et al. 1991; Bottom et al. 2005). To date, 27 distinct populations of salmonids along the Pacific coast of the United States have been listed as threat-

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ened or endangered under the Endangered Species Act. Given the ongoing anthropogenic impacts to Pacific coast estuaries and the recent Endangered Species Act listing of salmonid stocks, management and recovery efforts would be well served by an improved understanding of what characteristics of the estuarine habitat are important for growth and survival. Kareiva et al. (2000) used a demographic matrix model to demonstrate that even modest reductions in estuarine mortality would reverse current population declines in Snake River spring–summer Chinook salmon. Where should resource managers focus restoration efforts to reduce mortality in the estuary? Answering this question requires an improved understanding of how salmon use estuarine habitat.

Bottom et al. (2005) identified three general prey production–foraging habitat types important for juvenile Chinook salmon in the estuary: terrestrial–riparian, shallow benthic–epibenthic, and pelagic. To date, most studies of juvenile salmon habitat use have focused on terrestrial–riparian habitats such as river mouth emergent marsh areas (e.g., Fresh et al. 1981; Healey 1982*a*; Simenstad et al. 1982). Similarly, considerable research effort has focused on characterizing estuary-wide distribution patterns coincident with tidal cycles (Healey 1982*b*; Levy and Northcote 1982; Moser et al. 1991) and salinity gradients (Simenstad et al. 2000). Conversely, relatively few studies have investigated the distributions and relative abundances of salmon in relation to nearshore benthic–epibenthic estuarine habitats (an exception is Murphy et al. 2000). Benthic–epibenthic habitats in Pacific coast estuaries are important in the context of salmon management because they are a potentially productive source of prey (Bottom et al. 2005) and a source of physical structure (Murphy et al. 2000; Shaffer 2004). Additionally, these habitats are often modified extensively through aquaculture practices such as oyster culture (Dumbauld et al. 2001; Rumrill and Poulton 2004). An improved understanding of the behavioral ecology of Pacific salmon in relation to benthic–epibenthic habitats would undoubtedly aid in the effective multiple-use management of West Coast estuaries.

In this study, the fine-scale (<1 m resolution) movements of acoustically tagged juvenile Chinook salmon were monitored in a large (~4000 m^2) enclosure in Willapa Bay, Washington, USA, using a cabled acoustic positioning system (O'Dor et al. 1998; Ehrenberg and Steig 2003). The enclosure site was chosen to encompass representative patches of the principal benthic habitat components in Willapa Bay, native eelgrass (*Zostera marina*), non-native eelgrass (*Zostera japonica*), and oyster (*Crassostrea gigas*) beds and open substrate (e.g., mud flats), as well as an area of emergent vegetation composed of non-native smooth cordgrass (*Spartina alterniflora*). Following data collection, benthic habitat patches were digitized and subsequently linked to the positions recorded for each fish. These linked data sets were then used to model the influence of habitat on individual- and population-level behaviors.

Materials and methods

The work described in this study was carried out at the northern end of Nahcotta Harbor, Nahcotta, Washington. Fieldwork was conducted during July 2002 in cooperation with the Washington Department of Fish and Wildlife Shellfish Lab and the Port of Nahcotta. During the course of the study, the water temperature at the study site averaged 19.2 °C (SD = 1.6 °C). At the beginning and end of the experiment, the salinity of the water at the study site was measured at 24 and 26 PSU, respectively, at high tide. The Forks Creek Hatchery (Raymond, Washington) provided the juvenile Chinook salmon (Willapa stock, 0-aged fall Chinook smolts) for tagging under an agreement with the Washington Department of Fish and Wildlife. Two days prior to the initiation of the study, the subject fish were transported to Nahcotta Harbor using a transport container provided by Forks Creek Hatchery and subsequently placed in holding pens off the harbor dock. The transport container and holding pens were constantly aerated using oxygen cylinders and aeration stones.

Enclosure setup

The enclosure (Fig. 1) was constructed during a period of high tidal flux so that during the lowest tides, the enclosure site completely dewatered. The tidal timing of the experiment was such that the enclosure never completely dewatered while fish behavior was being monitored. The enclosure was constructed with 2 cm stretched mesh netting and 6.4 m 17-gauge galvanized tubing posts. Posts were placed every 5 m along the enclosure edge. A coated steel line was then attached along the top of the posts, and each end of the line was secured to the substrate above the high-tide line. The top of the net wall was subsequently attached to the top line with zip ties and secured to the substrate by laying polyvinyl chloride poles along the bottom of the net and staking them down. At the deepest part of the enclosure, the net wall was 3.5 m in height. The walls of the enclosure ran up onto shore beyond the intertidal zone. The enclosure bathymetry ranged along an even grade from ~1 m above mean high tide to 3 m below mean high tide. The total area of the enclosure from the deepest wall to mean high tide was ~4000 m^2. In July 2000 (~1 year prior to conducting the study), the existing oyster habitat at the enclosure site was augmented by creating a ~3 m × 3 m patch of oysters by relocating oysters from a nearby oyster reef.

Acoustic tracking

Tracking was performed using an acoustic tag tracking system (model 290; Hydroacoustic Technology, Inc., Seattle, Wash.). The tag receiver gathers acoustic signals on up to 16 separate channels and stores them on a computer hard-drive connected by serial port to the receiver. A total of nine hydrophones were used in this study. Hydrophone wires were run along the enclosure net wall up into a truck bed that housed the tag receiver. The relative positions of each hydrophone were determined by measuring the pairwise distances between all nine hydrophones. The arrival times of pulses from acoustic tags at each hydrophone were used to triangulate the locations of the tagged individuals using Hydroacoustic Technologies Incorporated proprietary software. Differences in pulse rates between tags were used to identify and track individual tags. Although the system is capable of tracking in three dimensions, this study did not

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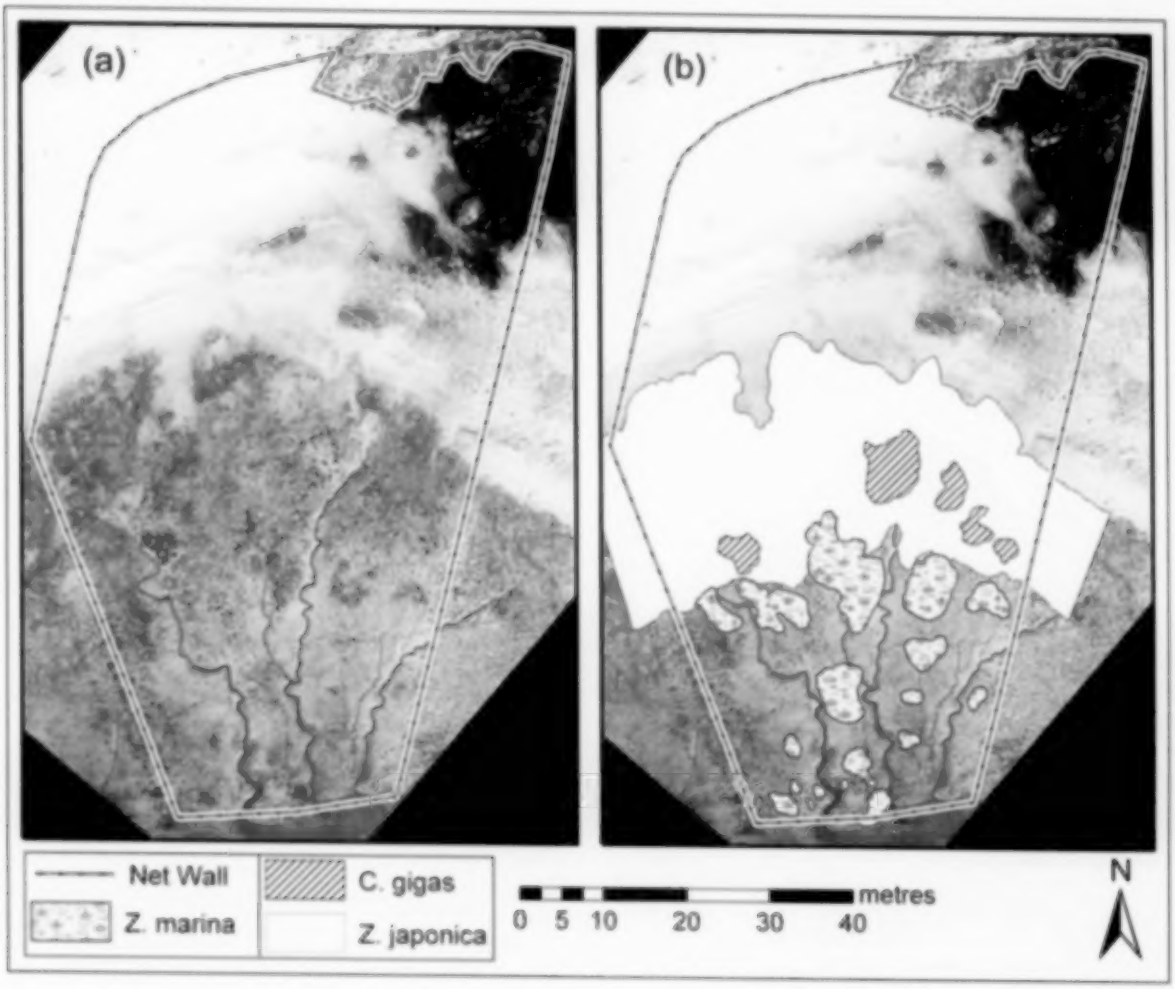
Fig. 1. (*a*) Orthorectified aerial photograph of the enclosure benthos taken during a low tide. (*b*) Photograph in (*a*) was used to digitize benthic habitat features in the enclosure. Non-native cordgrass habitat (dark area at the top right of the enclosure) was not digitized because no tagged fish swam into the area during the study. The high intertidal occupied by the cordgrass was submerged 2–3 h·day^{-1} during the study, with a maximum depth of ~0.75 m.



have enough vertical separation in the hydrophone array to resolve tag depth.

To evaluate error in two-dimensional (east–west and north–south) positioning, a single tag was placed consecutively at each of 11 known locations throughout the enclosure for a period of 5 min per location. These locations were specifically chosen to represent areas within the enclosure believed to have the poorest positional accuracy based on hydrophone geometry. Additionally, this error evaluation procedure was carried out when the tide was outgoing and the water was less than 1 m deep at the shallowest of the evaluated locations under the expectation that changes in water temperature, salinity, and noise interference would collectively contribute the most to position error. By taking this "worst-case" approach to error checking the tracking system, one could reasonably assume that error is no worse than, and perhaps generally better than, the assessed error. On average, system estimates of tag positions were less than 1 m from the true tag positions (mean = 0.69 m, SD = 0.39 m).

Fish tagging

Nineteen juvenile Chinook salmon were surgically implanted using microacoustic tags (model 795A; Hydroacoustic Technology, Inc.) weighing ~0.9 g in air (7 mm diameter, 17 mm length). Two of the implanted tags failed to activate properly, leaving 17 fish with active tags for the study (Table 1). Fish with the failed tags were released just outside the enclosure following recovery from surgery. Surgical procedures outlined in Adams et al. (1998) were used for implanting the acoustic tags in the gut cavity of fish. All implements and tags were bathed in antiseptic before each

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Table 1. Lengths and weights of tagged fish and mean posterior values for each of the fish-specific parameters used to characterize movement rates based on both day and night positions.

Length (mm)	Weight (g)	$\bar{\lambda}_i$	$\bar{n}_i$	$\bar{m}_i$	$\bar{o}_i$	$\bar{q}_i$	$\bar{p}_i$
119	19.4	5.15	-0.92	1.47	-0.30	-0.0157	-0.0764
119	19.6	5.58	0.86	0.04	1.32	0.0036	-0.1200
116	18.3	4.78	-0.92	0.16	-0.03	-0.0379	-0.1115
126	21.5	5.70	0.43	0.21	1.94	-0.0098	-0.1045
114	17.1	4.58	2.14	-0.60	1.72	-0.0115	-0.0912
115	18.1	5.05	-1.78	-0.39	0.52	-0.0191	-0.0239
113	15.6	5.09	-3.05	0.20	-0.73	-0.0205	-0.1177
118	19.2	2.01	-0.86	0.59	-0.30	-0.0450	-0.0522
114	16.2	5.81	-2.88	-0.82	-1.82	-0.0294	-0.1116
110	16.9	4.51	-0.95	0.24	-1.51	-0.0355	-0.1138
112	15.6	3.09	-0.99	0.22	2.62	-0.0172	-0.0880
112	15.3	4.75	-0.50	1.17	0.74	-0.0041	-0.0555
110	15.7	3.66	-1.03	1.54	-0.81	-0.0360	-0.1491
112	15.6	3.44	-0.53	-0.41	2.78	-0.0093	-0.0857
114	17.1	4.78	-2.31	-0.97	1.41	-0.0169	-0.0717
110	14.1	4.39	-2.91	0.20	0.52	-0.0166	-0.1462
114	16.1	2.58	-0.54	0.72	0.63	-0.0456	-0.0758
—	—	**4.41**	**-0.99**	**0.23**	**0.53**	**-0.0215**	**-0.0940**

Note: The units of $\bar{\lambda}_i$ (base rate of movement), $\bar{n}_i$ (rate adjustment for native eelgrass), $\bar{m}_i$ (rate adjustment for non-native eelgrass), and $\bar{o}_i$ (rate adjustment for oysters) are metres moved per 30 s period. Values for $\bar{q}_i$ and $\bar{p}_i$ represent exponential rates of change in movement as a function of net proximity and location depth, respectively. The final row (bold) gives the mean posterior hyperparameter values associated with each of the parameters.

surgery. Fish were anesthetized with tricainemethanesulfonate (MS 222) prior to surgery in a rapid anesthetic bath. Once a fish lost motor function and did not respond to being bent at midbody, its weight and fork length were measured, and then it was placed ventral side up in a plastic cradle. Each fish was supplied reduced anesthetic over its gills through plastic surgical tubing inserted in the mouth during surgery. A small incision was made to open the abdominal cavity, the tag was inserted, and then the incision was sutured and covered with triple-antibiotic ointment. Approximately three-quarters of the way through each surgery, the solution flowing over the gills of the fish was switched to salt water. Throughout the surgery, the opercular activity of the fish was monitored, and if any significant slowing was evident, the switch to water was made immediately. Following surgery, the fish were placed in a recovery bath with oxygen bubbling through it for 30 min and then transferred to a pen near the enclosure site where they were held for at least 12 h prior to release in the enclosure.

Habitat characterization

The enclosure habitat was digitized using a high-resolution aerial photograph of the enclosure location taken 1 month after the conclusion of the study at a time when the low tide exposed the entire enclosure site. Before the photograph was taken, orange cones were placed on each of the hydrophone positions. The aerial photograph was subsequently scanned and orthorectified to the hydrophone coordinate system in Arcview 3.2 (ESRI, Redlands, California) using the IMAGEWARP extension, with each of the orange cones as reference points in the image. Using the orthorectified image, mutually exclusive polygons were drawn around all patches of oysters, native eelgrass, and non-native eelgrass (Fig. 1). All salmon paths were then brought into the geodatabase and all positions within each path were subsequently assigned habitat values of 1 or 0 for each benthic habitat type depending on whether the position fell over the given habitat type. Additionally, for each position, the absolute depth (the height of the substrate relative to the bottom of the lowest part of the enclosure), the relative water depth (the depth of water over the position given the absolute depth and tide height at the time of the position), and net-wall proximity (closest straight-line distance between each position and the enclosure net wall) were calculated. The result was thus a matrix of positions for each fish that included *XY* coordinates, binary values indicating presence or absence each benthic habitat type, and continuous values describing depth and net-wall proximity.

Modeling

Markov chain Monte Carlo simulations were conducted using a hierarchical Bayesian state–space model of juvenile salmon movement to investigate the influence of habitat on behavior. Although state–space models are widely used in engineering for analyzing data in series, their utility in analyzing animal tracking data has only recently been demonstrated (Jonsen et al. 2003; Morales et al. 2004; Jonsen et al. 2005). State–space models are useful for animal tracking data because they can simultaneously account for (*i*) technology-based (measurement) error sources in the estimation of true locations, (*ii*) random variability in directional movement, and (*iii*) state variables that affect movement (in this case, characteristics of habitat in the enclosure). Moreover, state–space models address issues of serial autocorrelation in path data by explicitly dealing

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with transition probabilities between animal locations as a function of underlying location attributes. Using a state–space model within a meta-analytic framework allowed for integration across multiple individual animal tracks in the estimation of population-level behaviors.

The state–space model formulation used followed that of Jonsen et al. (2003). Using their conventions, the two model components are the transition and measurement equations (eqs. 1 and 2, respectively):

$$(1) \qquad \alpha_{i,t+1} = \alpha_{i,t} + \eta_{i,t}$$

$$(2) \qquad y_{i,t} = \alpha_{i,t} + \varepsilon_{i,t}$$

where α_i represents the matrix of unobserved true locations of each fish i in two-dimensional space (state variables), η_i represents the matrix of process noise, y_i represents the matrix of observed locations, and $\varepsilon_i \sim (0, \sigma_\varepsilon)$ represents the matrix of errors in observed locations. Here, $\eta_{i,t} \sim (0, \sigma_{i,t})$, where $\sigma^2_{i,t}$ is the variance in movement of fish i defined in part by the habitat characteristics of the location at time t. The model assumed equivalence in observation error in two dimensions to avoid multiplicatively increasing the parameter hypervolume of the full model and because there were insignificant differences in variance between dimensions (paired t test, $p = 0.17$). Akaike's information criterion values were used as a guide in constructing appropriate habitat components of σ. Because of the size of the data set, model-fitting tests were conducted on individual fish while excluding observation error rather than running separate models within the entire meta-analytic framework. At the outset, adjustments to σ associated with *Z. japonica*, *Z. marina*, and *C. gigas* were included because these benthic habitats are clearly important to estuarine resource management in Willapa Bay and elsewhere (Ruesink et al. 2006). Additional factors for absolute depth (hereafter referred to simply as depth) and distance to enclosure wall improved model fit for all fish. The addition of a linear time adjustment to σ marginally improved model fit for the two tagged individuals that survived the longest in the enclosure but did not improve the fit for the remainder of the tagged fish. The meta-analytic model therefore did not include a time factor. Variance in movement for each individual i at each location t was thus parameterized as follows:

$$(3) \qquad \sigma_{i,t} = (s_i + m_i \times \text{japonica}_{i,t} + n_i \times \text{marina}_{i,t} + o_i \times \text{gigas}_{i,t}) \times e^{-p_i \times \text{depth}_{i,t}} \times e^{-q_i \times \text{net}_{i,t}}$$

By default, s_i reflects variance in movement over open substrate. Because values of *Z. japonica*, *Z. marina*, and *C. gigas* are binary in the data matrix, they act as dummy variables for the parameters m_i, n_i, and o_i, respectively. These parameters represent additive adjustments to s_i associated with the different benthic habitat components. The parameters p_i and q_i determine how rapidly the distance moved at each time step changes as an individual moves shallower in the enclosure or farther away from the net wall, respectively. In the meta-analytic formulation of the model outlined by eqs. 1 and 2 above, each parameter describing $\sigma_{i,t}$ is drawn from an associated normal distribution defined by hypermean parameters ($\hat{s}$, $\hat{m}$, $\hat{n}$, $\hat{o}$, $\hat{p}$, and $\hat{q}$) and hypervariance parameters (σ^2_s, σ^2_m, σ^2_n, σ^2_o, σ^2_p, and σ^2_q). These hyperparameters define the population-level influence of habitat features on the fine-scale movements of Chinook salmon by combining information across all tagged individuals in my study.

To account for the possibility that fish behaved differently during the day than at night, three separate model runs were conducted using the following data sets: (*i*) only nighttime positions (all positions collected between 1 h after sunset and 1 h prior to sunrise), (*ii*) only daytime positions, and (*iii*) all daytime and nighttime positions. Each model run incorporated uninformative priors (mean = 0, variance = 1000) for all parameters and hyperparameters used in the formulation of $\eta_{i,t}$ and informative priors (mean = 0.695, variance = 0.478) for σ_ε (observation error) based on the error in position estimates for the test tags. R-CODA (convergence diagnosis and output analysis) convergence statistics were used to ensure appropriate posterior chain lengths and thinning.

Results

All 17 tagged fish released into the enclosure were apparently killed by predators during the course of the study. Belted kingfisher (*Megaceryle alcyon*), great blue heron (*Ardea herodias*), and great egret (*Ardea alba*) were observed hunting in the enclosure. Caspian tern (*Sterna caspia*) probably also hunted in the enclosure, although they were not observed doing so. Because the enclosure net wall was put in place when the study site was completely dewatered, it is unlikely that tagged fish were killed by predatory fishes such as sculpin (Cottoidea). On average, fish survived ~60 h (2.5 days), with the fish that survived the longest spending nearly 7 days in the enclosure. Because the acoustic system updated fish locations approximately every 3 s, it was possible to determine where predation events took place in the enclosure. All 17 individuals were apparently preyed upon while over open substrate.

The plots of fish positions in the enclosure (Fig. 2) clearly showed high position densities above native eelgrass patches, near the net wall, and in the deeper parts of enclosure. The time-series paths of individuals appeared to show a periodic "resting" behavior over native eelgrass, where fish would stay virtually motionless for long periods, sometimes for an hour or more in eelgrass stands less than 2 m in diameter. These periods of rest did not appear to be correlated with tidal stage or time of day. The influence of non-native eelgrass and oysters on the behaviors of tagged individuals was not visually apparent based on plots of fish positions or by looking at the time-series paths of individuals. No tagged fish ever ventured into the non-native cordgrass habitat during the study period.

The state–space model results were in general agreement with the visual interpretation of the plotted fish positions. There were no marked differences between the posterior distributions of the model hyperparameters from the day and night data sets (Fig. 3). Considering the model run using all of the data (both day and night positions) (Fig. 3*c*; Table 1), the data provide strong support for a behavioral "slow-down" in smolts while over native eelgrass based on the posterior distribution of the hyperparameter $\hat{n}$. Conversely, the model results show limited support for the notion that Chinook salmon speed up over native eelgrass. The posterior

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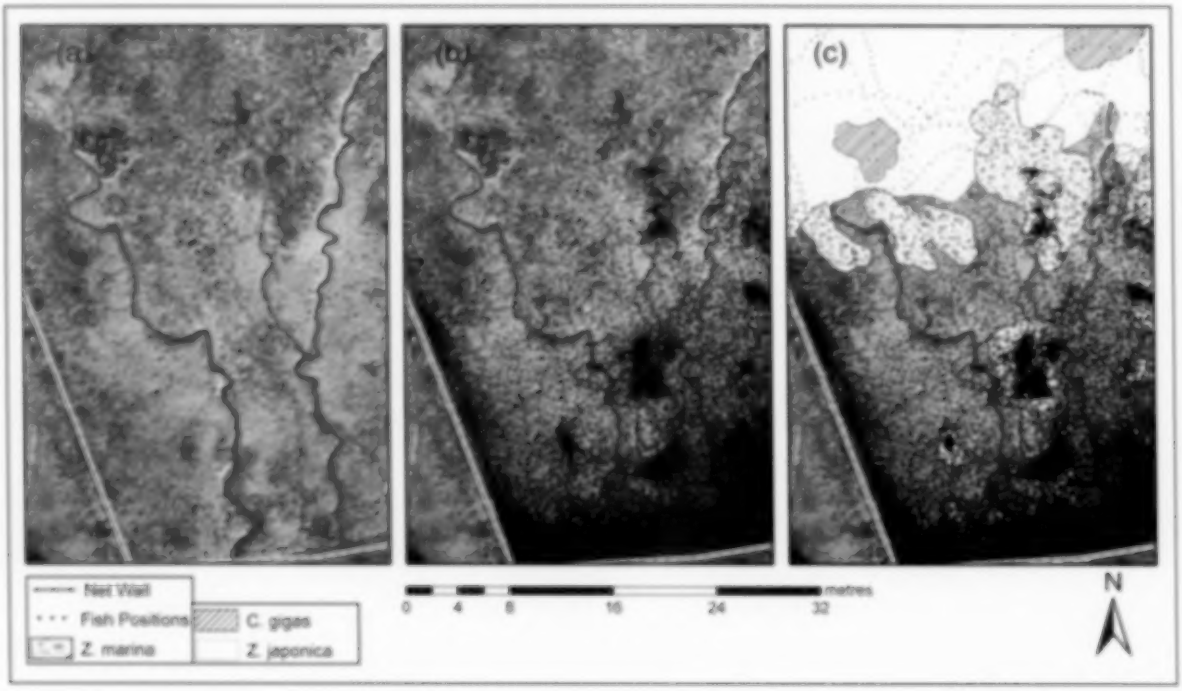
Fig. 2. (*a*) Map of the lower-left (southwestern) corner of the enclosure. (*b*) Map including all of the recorded positions of the tagged individual that survived the longest during the study. (*c*) Map including an underlay of polygons representing the benthic habitats in the enclosure. Note that areas of increased position densities occur over patches of native eelgrass, near the net wall, and in the deeper (southern) area of the enclosure.



values for $\bar{p}$ and $\bar{q}$ were both nearly exclusively negative, demonstrating strong support for the notion that Chinook salmon slow down as they get deeper in the enclosure and closer to the net wall.

The loss of all tagged individuals due to predation during the study afforded the opportunity to investigate the relationship between behavioral responses to native eelgrass and survival times (Fig. 4). The software program WinBUGS (Lunn et al. 2000) was used to fit the following simple function (chosen based on Akaike information criterion model selection):

$$(4) \qquad \text{days}_i = a \times \log(\theta_i) + b$$

where days_i is the duration of time survived for each individual and θ_i is the mean posterior value of n_i for each tagged individual. Uninformative priors for both the slope (a) and intercept (b) parameters were used. A plot is presented of the curve defined by the mean posterior intercept and slope values and a kernel density plot of the slope parameter posterior values (Fig. 3). The bulk of the posterior slope values were negative (Fig. 4*b*), supporting the hypothesis that fish that slowed down more in native eelgrass patches were less susceptible to predation during the study.

Discussion

Efforts to manage estuarine habitat to improve Pacific salmon growth and survival must be approached from a landscape perspective (Simenstad and Cordell 2000; Haggarty and Healey 2002; Bottom et al. 2005). Simenstad and Cordell (2000) proposed a conceptual framework for evaluating estuary habitat for Pacific salmon in terms of both opportunity (i.e., accessibility based on geography, oceanography, flow regimes, etc.) and capacity (i.e., opportunity for growth and survival based on biological interactions such as competition and predation). Ultimately, determining the opportunity and capacity afforded by an estuarine landscape requires both broad geographic information about the connectivity of habitat patches and an understanding of how the specific habitat components that comprise patches mediate biological interactions. Previously, studies addressing this latter information were limited by the tools available for collecting behavioral data at fine spatial and temporal scales in the estuary. The research presented here is the first to link benthic habitats with near-continuous fine-scale observations on multiple individuals over multiple days. Based simply on location point densities plotted over the benthic habitat of the enclosure, it appeared that tagged fish tended to stay deeper in the enclosure, near the net wall, and in patches of native eelgrass. The state–space modeling effort confirmed these relationships, expressed as adjustments to rates of movement.

Differences in position densities or rates of movement within a habitat type often, but not always, reflect differences in habitat quality (van Horne 1983; Winker et al. 1995). For instance, mobile animals may slow down over certain habitats owing simply to navigational hazards, regardless of habitat quality. The tagged fish in this study routinely re-

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Fig. 3. Box plots of posterior values for the hyperparameters representing benthic habitat specific adjustments to population-level Chinook salmon (*Oncorhynchus tshawytscha*) movement rates using (*a*) daytime positions, (*b*) nighttime positions, and (*c*) both. For ease of interpretation, the posterior values for each benthic habitat hyperparameter are expressed as percent adjustments to the mean posterior value of the $\bar{s}$ hyperparameter (the base movement rate over open substrate). Negative values for a given habitat indicate that fish slow down; positive values indicate that fish speed up. Horizontal lines at zero on the *y* axes are provided to clarify the extent to which the posterior distributions are negative versus positive. The upper and lower ends of the boxes represent the 75th and 25th percentiles, respectively, and the whiskers depict the extent of the data.

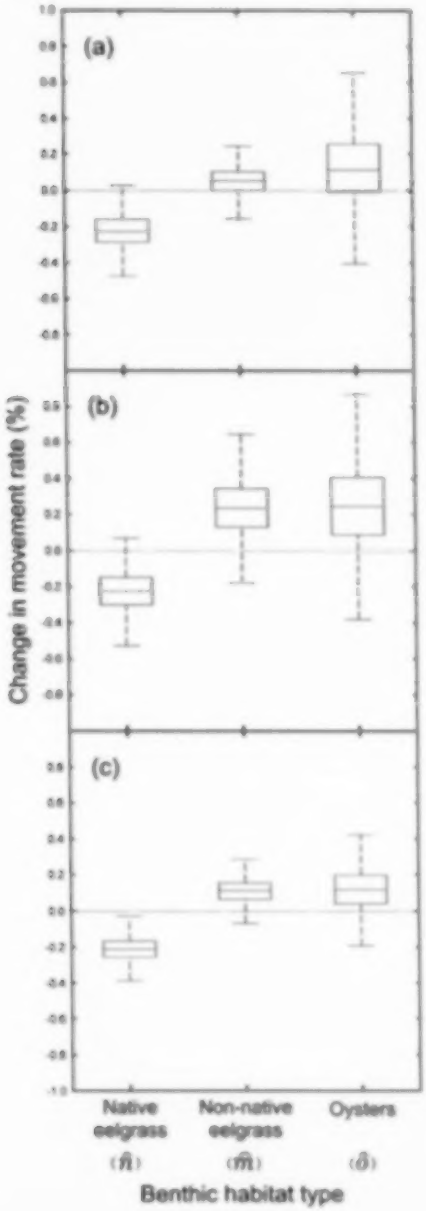
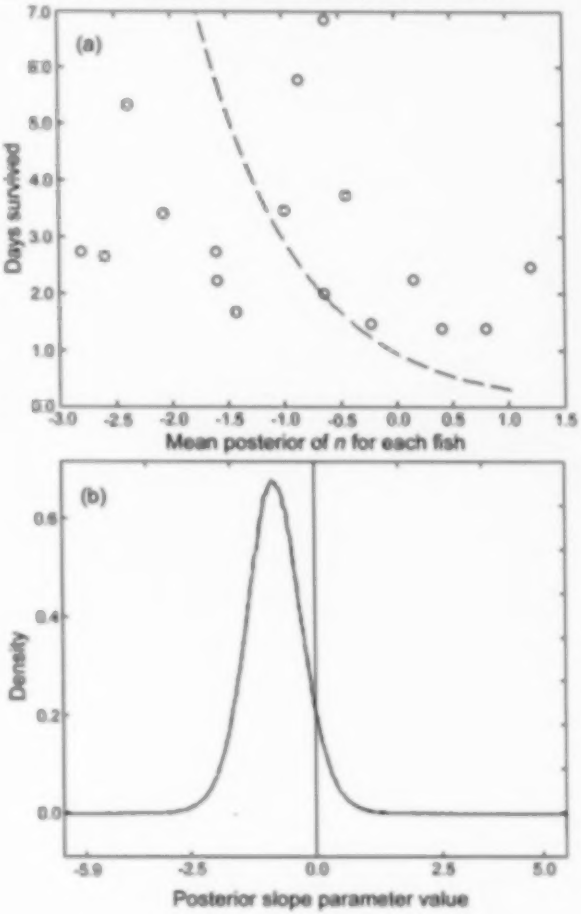


Fig. 4. (*a*) Scatterplot of the mean posterior values for $\bar{n}_i$, the adjustment to the rate of movement (metres per 30 s period) for each tagged individual while in native eelgrass, as a function of time (days) that each individual survived. The broken line represents the curve resulting from mean posterior values of the slope and intercept based on fitting the linear relationship between and log-transformed survival times (days). (*b*) Posterior distribution of the slope parameter. The plot includes a vertical line at zero on the *x* axis to demonstrate that most of the posterior density falls below zero.



mained in relatively small native eelgrass patches for long periods of time, suggesting a behavioral preference for the habitat rather than a simple mechanistic effect of habitat on movement. Ideally, the survival and production characteristics of habitats should be investigated to determine the extent to which habitat use or preference reflects habitat quality (van Horne 1983). Position densities, rates of movement, and patterns of survival in this study were all consistent with the hypothesis that native eelgrass is an important benthic habitat for juvenile Chinook salmon in the estuary.

The propensity of tagged individuals to remain in the deeper parts of the enclosure coincides with the results of previous large-scale netting studies that found that individuals of the size used in this study tended to be found in the deeper tidal channels of estuaries (Myers and Horton 1982; McCabe et al. 1986; MacDonald et al. 1987). Similarly, pre-

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vious studies have demonstrated that fish of the size tagged move over much large areas than that encompassed by the enclosure on a daily basis (Levy and Northcote 1982). As such, it is not surprising that the tagged individuals spent a large proportion of their time along the net wall. The state–space model employed in this study explicitly accounted for and factored out the influence of depth and net-wall proximity in assessing the influence of benthic habitat on behavior. However, reducing habitat features such as depth to a single-parameter component of an equation describing movement may not capture the entirety of the complex and context-dependent influences of such habitat attributes. Given the lack of an obvious ecological explanation for the model support for increased movement rates in non-native eelgrass and oyster habitat and the fact that these habitats were specific to the mid-depth ranges of the enclosure, it is possible that the model results at least partially reflect an effect of depth not fully captured by the parameter q in the equation. In addition to the clear influence of the enclosure structure on the movement of fish, it is possible that the acoustic tags also modified fish behavior and susceptibility to predation (Bridger and Booth 2003). It seems unlikely, however, that the influence of the tags modified fish behavior to such a degree that responses to gross habitat features were substantially altered.

Juvenile Chinook salmon may slow down in native eelgrass because the habitat affords better foraging opportunities, better cover from predators, or both. Diet composition studies in both Willapa Bay (Dumbauld 2005) and Puget Sound (Brennan et al. 2004) suggest that Chinook salmon of the size used in this study feed predominantly on terrestrial insects, a food source that likely is not mediated by benthic habitat. Moreover, Hosack et al. (2006) found no difference between diversity and abundance of epibenthic fauna between eelgrass habitat and oyster habitat in Willapa Bay. These previous findings suggest that prey availability is probably not the principal reason that juvenile Chinook salmon slow down in native eelgrass habitat. On the other hand, the apparent relationship between native eelgrass use and the duration of survival in the enclosure suggests that native eelgrass plays an important role in predator avoidance. This is anecdotally supported by the fact that none of the tagged fish was preyed upon while in native eelgrass patches. Native eelgrass blades are taller and thicker than non-native eelgrass and therefore provide more vertical structure in the water column in which to hide. Additionally, native eelgrass tends to occur deeper in the intertidal than non-native eelgrass and may thus be ecologically more available as cover habitat given the proclivity for deeper water that Chinook salmon of the size tagged demonstrate.

Wild Chinook salmon smolts may not necessarily exhibit the same behavioral responses to habitat exhibited by the hatchery fish used in this study. Hatchery-reared salmonids tend to have lower survivorship than wild salmonids (Wales 1954; Kostow 2004). These differences have been attributed principally to the fact that hatchery fish have less well developed predator avoidance behaviors (Dickson and MacCrimmon 1982; Olla et al. 1998; Berejikian et al. 2003), tend to be more surface-oriented (Vincent 1960; Reinhardt 2001), and have elevated stress levels owing to handling (Olla and Davis 1989). This latter effect was unquestionably amplified in this study owing to transport, tagging, and introduction to a novel environment. Taken together, these hatchery-specific traits likely increased the susceptibility of the fish in this study to predation and may partially explain the high rate of mortality observed. Moreover, the fact that "naïve" smolts were used as subjects in this study may have masked even stronger behavioral responses to habitat (Healey and Reinhardt 1995).

Although a landscape perspective is critically important in the evaluation of habitat quality for Pacific salmon, it is difficult to enforce legislative rules aimed at preserving landscape features such as habitat matrices and connectivity. For this reason, management of estuarine habitats typically proceeds through the establishment and enforcement of simple conservation rules such as "no net loss of native eelgrass"; presumably, if well conceived, these rules scale across an estuary to approximate landscape management. An understanding of the relative importance of benthic habitat components for growth and survival will undoubtedly aid managers in the development of such scalable management actions. In other words, an assessment of the capacity and opportunity of benthic habitats requires an understanding of the ecological and physiological responses of juvenile salmon to habitat features. This is particularly true given that nearshore intertidal habitats in many Pacific coast estuaries are extensively used and manipulated by the aquaculture industry.

Aquaculture practices in Willapa Bay alter native eelgrass stands but do not exclude them. Approximately 10% of the total area of Willapa Bay is intensively cultured for bivalves (Feldman et al. 2000), and 10% of the Bay is covered by native eelgrass (Borde et al. 2003); the extent to which these benthic features overlap in the Bay is currently unknown. Even intensively cultivated areas of Willapa Bay have some coverage of native eelgrass (approximately one-third that of uncultivated sites; H.M. Tallis, Department of Biology, University of Washington, Seattle, WA 98195, USA, unpublished data), suggesting that the native eelgrass persists on cultivated intertidal areas, albeit with patchier distributions and lower percent cover. The overall mobility of Chinook salmon coupled with their ability to make use of relatively small stands of native eelgrass may allow for behavioral compensation in response to the reduction in native eelgrass resulting from cultivation. On the other hand, the extent to which compensatory behaviors can mitigate the impact of a reduction in habitat quality on growth and survival undoubtedly depends on the extent to which habitat quality is reduced. Future efforts to explicitly address differences in behavior across a gradient of habitat availability and quality may identify where such compensatory thresholds lie. The apparent similarity in habitat capacity provided by non-native eelgrass and oysters suggests that the common practice of assuming that native and non-native eelgrasses are ecologically equivalent may unduly burden the aquaculture industry during efforts to implement "salmon-friendly" management practices.

Life history traits specific to individuals or stocks play a fundamental role in the evaluation of habitat opportunity and capacity, as these traits dictate factors such as outmigration timing and estuarine residency (Bottom et al. 2005). Relatively large fish were used in this study because they

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were readily available from a nearby hatchery and because the size of the acoustic tags precluded the use of smaller fish. Although fish of the size used (<135 mm) are typically found in water shallower than 4 m (Dawley et al. 1981), they have a shorter estuarine residence than smaller subyearling migrants (Bottom et al. 2005) and are less dependent on shallow rearing habitats such as emergent marsh, tidal creeks, and associated dendritic channel networks (Levy and Northcote 1982; Gray et al. 2002). From a management perspective, it may therefore be tempting to downplay the importance of fine-scale benthic habitats in favor of larger-scale estuarine features such as deep tidal channels and salinity gradients for smolt-sized fish. However, the strong influence of benthic habitat on the behaviors of larger Chinook salmon juveniles identified in this study suggests that the benthic habitat plays an important role in survival during outmigration and should not be discounted in preservation and restoration actions aimed at conserving and recovering Chinook salmon stocks.

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Influence of origin on migration and survival of Atlantic salmon (*Salmo salar*) in the Bay of Fundy, Canada

Gilles L. Lacroix

Abstract: Atlantic salmon (*Salmo salar*) smolts of wild and hatchery origins (n = 522) were tagged with ultrasonic transmitters and monitored at successive arrays of submerged receivers during migration from five watersheds in three regions of the Bay of Fundy (BoF), Canada. Two of the regions had endangered inner BoF salmon populations. Migration success of postsmolts leaving the BoF varied widely among 13 groups monitored (3%–70%) and was influenced by behaviour and passage time. Region of origin was the key variable in habitat-specific survival models selected using the Akaike information criterion. Rearing origin, migration and release timing, and smolt size were important variables in some habitats. Estimated survival rates (overall and habitat specific) differed markedly among salmon populations of different regions. Mediocre estuarine survival of smolts (0.54) from the outer BoF region affected overall survival (0.66). Poor survival (0.21) in coastal areas of the distant inner BoF region and mediocre survival in other habitats resulted in low overall survival (0.06) that severely limited the potential for population recovery. Potential predators were abundant in habitats where survival was lowest. High survival of salmon from the intermediate inner BoF region in all habitats (0.81–0.93) was not responsible for their failure to return.

Résumé : Des saumoneaux du saumon atlantique (*Salmo salar*) d'origine sauvage et de pisciculture (n = 522) ont reçu des émetteurs ultrasoniques et ont pu être suivis dans divers réseaux de récepteurs submergés durant leur migration à partir de cinq bassins versants dans trois régions de la baie de Fundy (BoF), Canada. Deux des régions possèdent des populations menacées de saumons de la zone intérieure de la BoF. Le succès de la migration des poissons après le stade saumoneau qui quittent la BoF varie considérablement (3–70 %) dans les 13 groupes suivis et il est influencé par le comportement et le temps de passage. La région d'origine est la variable principale dans les modèles de survie spécifiques à l'habitat retenus à l'aide du critère d'information d'Akaike. La région d'élevage, les moments de la migration et de la libération, ainsi que la taille des saumoneaux sont des variables importantes dans certains habitats. Les taux estimés de survie (globaux et spécifiques à l'habitat) varient de façon marquée chez les populations de saumons des différentes régions. La survie médiocre (0,54) dans l'estuaire des saumoneaux de la région extérieure de la BoF affecte la survie globale (0,66). La survie faible (0,21) dans les régions côtières de la région intérieure éloignée de la BoF et la survie médiocre dans les autres habitats a comme conséquence une survie globale faible (0,06) qui limite sérieusement le potentiel de récupération de la population. Les prédateurs potentiels abondent dans les habitats où la survie est la plus faible. Une survie élevée (0,81–0,93) des saumons dans la région intérieure intermédiaire de la BoF dans tous les habitats n'est pas responsable du non retour des saumons.

[Traduit par la Rédaction]

Introduction

The dramatic decline in abundance of Atlantic salmon (*Salmo salar*) populations from both eastern and western North Atlantic countries in the late 20th century is generally attributed to increased mortality at some time between smolt entry into seawater and adult return to the river. Exceptions would be populations affected by commercial exploitation or by extensive freshwater habitat loss from acidification, obstructions, and pollution. Although mortality is deemed to be highest early in the marine phase as postsmolts migrate from coastal habitat to feeding grounds, there are no empirical data to support this assumption.

A new approach using arrays of underwater receivers to detect ultrasonic transmitters within individually tagged salmon during migration in freshwater and marine habitats was developed to address knowledge gaps during this period (Voegeli et al. 1998; Lacroix and Voegeli 2000; Lacroix et al. 2005). This provided a mechanism to measure migration success at intervals along the migration route. The Bay of Fundy (BoF) on the east coast of Canada was considered an ideal location to apply this method for the following reasons: basin topography and hydrography were suited for the use of long arrays or "curtains" of underwater receivers to close off sectors of the bay and accurately monitor fish migration (Lacroix and Knox 2005; Lacroix et al. 2005), salmon populations from inner BoF rivers, listed as endangered in 2001 (Committee on the Status of Endangered Wildlife in Canada 2006), were representative of an extreme, rapid downturn in adult returns (Amiro 2003; Ir-

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vine et al. 2005), salmon populations in outer BoF rivers of the Saint John River system had not declined as much as in inner BoF rivers and provided opportunities for comparison (Jones et al. 2006), and hatchery-reared salmon smolts stocked in both inner and outer BoF rivers as part of recovery and conservation programs offered additional possibilities for comparing early marine performance.

This study used large-scale deployments of underwater receivers in estuarine habitat and in the BoF to monitor migrating young Atlantic salmon from 13 different groups tagged with ultrasonic transmitters. The goals were to accurately measure the migration success of salmon of different origins from the BoF, identify periods and habitats where mortality occurred, and estimate survival to predict the impacts on adult salmon returns. Hypotheses concerning proposed relationships between the survival of emigrating salmon and geographic and genetic origin, rearing origin and fish size, run timing and release date, and migration distance and behaviour were examined. Habitat-specific losses of salmon were used to evaluate some of the hypothesized causes for increased mortality and the decline in abundance of North American Atlantic salmon (Cairns 2001). For salmon from inner BoF rivers, these included (*i*) disruption of smolting physiology, (*ii*) changes in migratory behaviour, (*iii*) interaction with Atlantic salmon farms, (*vi*) capture by intercepting fisheries, (*v*) habitat suitability, and (*vi*) abundance of predators.

Materials and methods

Electronic tagging

Atlantic salmon of wild and (or) hatchery origin from three different regions of the BoF were monitored using ultrasonic transmitters and receivers (VEMCO Ltd., Shad Bay, Nova Scotia). They were tagged as smolts and monitored until they left the rivers after which time the same tagged fish continued to be monitored as postsmolts through the BoF. They included salmon from two distant inner BoF rivers (Stewiacke and Gaspereau) up in Minas Basin, Nova Scotia, two intermediate inner BoF rivers (Upper Salmon and Big Salmon) along the New Brunswick coast, and two outer BoF rivers (Saint John and Nashwaak) of New Brunswick (Fig. 1*a*). Genetic variation among salmon of these regions was found to be much greater than within regions with obvious genetic differentiation between populations of the three regions (Verspoor et al. 2002, 2005).

Wild smolts were captured throughout the migration period using floating rotary-screw fish traps (E.G. Solutions Inc., Corvallis, Oregon) located in freshwater near the head of tide in the Upper Salmon and Big Salmon rivers in 2001 and 2002 (Flanagan et al. 2006) and in the lower Nashwaak River in 2002 (Chaput and Jones 2004) (Fig. 2*a*). Smolts were tagged by surgically implanting uniquely coded transmitters (V8SC-69 kHz with R256 coding, 1L or 6L battery options, and 142 dB power output) as described by Lacroix et al. (2004*a*, 2005). Most smolts were captured overnight, tagged in situ in the morning (<24 h after capture), and then released after recovery (1–3 h after surgery).

Hatchery-reared salmon smolts of different origins (Saint John River mixed stock of upper tributaries in 2001 and 2002 and native stocks from the Stewiacke, Gaspereau, Big Salmon, and Nashwaak rivers in 2002) were similarly tagged at the hatcheries several days before release. Smolts were transported and released in freshwater with untagged smolts at sites normally used for stocking. Additionally, tagged hatchery smolts were released on three occasions in the Big Salmon River to examine the effect of delays in migration time (day of year (DOY) 149, 156, and 168) (Fig. 2*a*).

In all, 13 different groups of smolts were tagged. The size of transmitters was similar for each smolt group (mean length = 20–24 mm, mean weight in air = 3.1–3.6 g), but the mean length and weight of smolts differed among rivers and stocks (Fig. 2*b*). In rivers where both wild and hatchery smolts were tagged, the wild smolts were always smaller. However, some hatchery smolts (Stewiacke River) were as small as the smallest wild groups (Big Salmon River (2001) and Nashwaak River (2002)), and they were smaller than other hatchery smolts including those (Gaspereau River) reared under identical conditions at the same hatchery. Transmitters were, in proportion to mean smolt length and weight, within acceptable limits for transmitter retention and long-term survival (Lacroix et al. 2004*a*); the proportions (mean = 10%–14% for length, mean = 3%–8% for weight) were greatest in the small wild smolts and lowest for the largest hatchery smolts (Fig. 2*c*). A mean random code repetition interval of 45 s (range = 20–90 s) helped increase expected transmitter life to 3–4 months (duration verified in the field >4 months) while ensuring a high probability of detection (Lacroix and Voegeli 2000).

Telemetry monitoring network

The passage of tagged smolts in the rivers was continuously monitored (period = 3 months, late April to late July) by longitudinal arrays of submersible ultrasonic receivers (VR2-69 kHz with high bias setting to boost acoustic range and custom code map to ensure regionally unique codes) deployed at fixed sites near the release sites in freshwater or at the head of tide, at intervals within the estuaries (at least one intermediate site in short estuaries), and at the mouth of rivers (Fig. 1*a*). Receivers were either hung 1–2 m off the bottom from deepwater floats attached to anchored and weighted snag lines or attached directly to weights on the bottom in shallow areas, except at the mouth of the Saint John River where receivers were hung 8–10 m below the surface from several piers. Sites where the channel narrowed markedly were selected, and at each site, a pair of receivers was deployed in the channel <500 m apart along the river to increase the probability of transmitter detection and provide information on direction of movement.

The passage of postsmolts with transmitters through the BoF was continuously monitored (period = 4–6 months, late April to September–October) by linear arrays of submersible ultrasonic receivers (VR2 and some VR1-69 kHz with similar custom settings and detection range (Lacroix and Voegeli 2000)) moored at fixed sites and reaching from shore to shore across the hypothetical boundary between the inner and outer BoF based on major regional genetic distinction between Atlantic salmon groups from different rivers (Verspoor et al. 2002) (52–54 receivers) and across the Grand Manan Channel and Grand Manan Basin that link the outer BoF to the northern Gulf of Maine at the level of Grand

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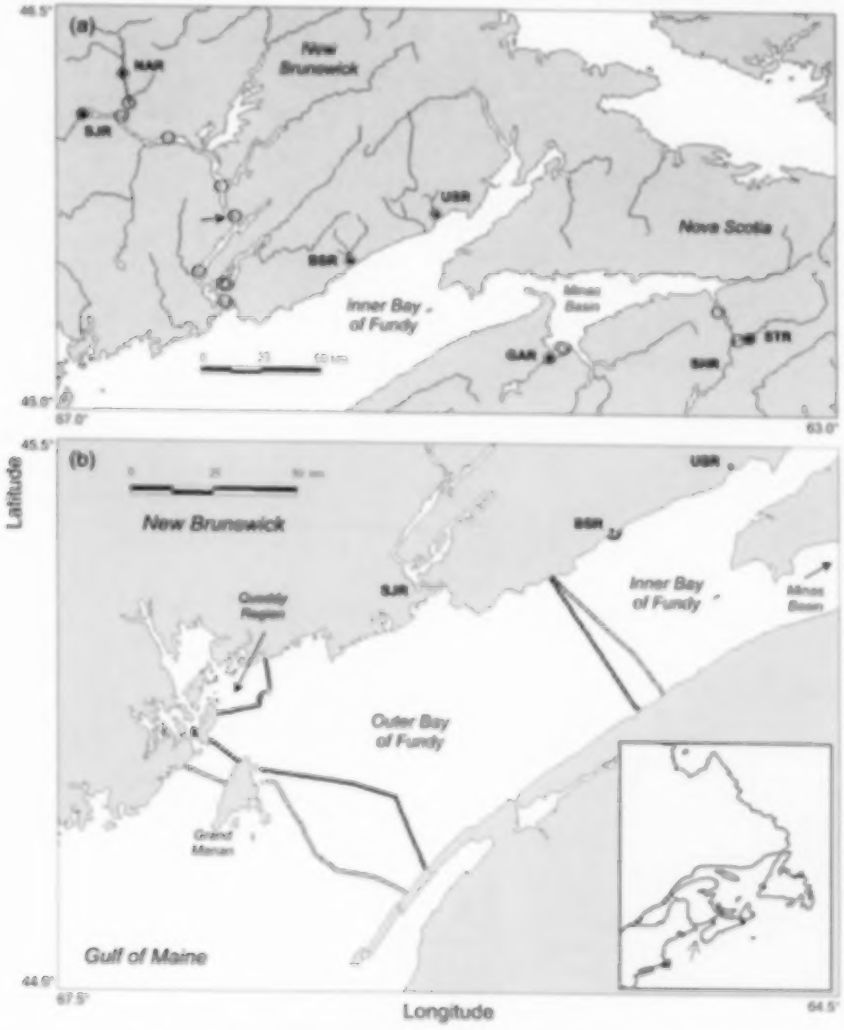
Fig. 1. Maps of the Bay of Fundy on the east coast of Canada (inset, Fig. 1*b*) showing (*a*) the capture and release sites (solid circles) of Atlantic salmon (*Salmo salar*) smolts tagged with transmitters and the location of clusters of ultrasonic receiver in rivers (open circles) and (*b*) the location of receivers in marine arrays deployed in 2001 (shaded circles) and in 2002 (open circles) for monitoring the migration of postsmolts with transmitters. River abbreviations: SJR, Saint John (boundary of the lower estuary marked by the arrow); NAR, Nashwaak; BSR, Big Salmon; USR, Upper Salmon; STR, Stewiacke; SHR, Shubenacadie; GAR, Gaspereau.



Manan Island (75–79 receivers) (Fig. 1*b*). In 2001, additional arrays of receivers were also deployed in the coastal area immediately surrounding the mouth of the Big Salmon River (six receivers) (Fig. 1*b*) to examine the hypothesis that smolt mortality was significant as they entered salt water and across access points to the Quoddy Region in southwest New Brunswick (30 receivers) (Fig. 1*b*) to examine the hypothesis that postsmolts from inner BoF rivers migrated inside the Quoddy Region and failed to leave because they were adversely affected by close contact with the many Atlantic salmon farms in that region (data from five VR2 receivers located in Lubec Narrows were provided by T.F. Sheehan, Northeast Fisheries Science Center, 166 Water Street, Woods Hole, MA 02543, USA).

The majority of receivers in the BoF were suspended 15–20 m below the surface (less at shallow sites) from surface buoys moored as described by Lacroix and Voegeli (2000). However, in areas of ship and whale traffic on the outer bay array, receivers were hung 2–3 m off the bottom from deepwater floats attached to anchored and weighted snag lines. Whale-safe features such as breakaway links (Plante's Lobster Escape Vents Inc., Somerville, Maine) at several key points or sinking lines were used. The detection range of receivers and transmitters in different marine areas under a variety of sea states, tidal conditions, and deployment depths was determined from extensive testing before the study to set the spacing between receivers (Lacroix and Voegeli 2000; Lacroix et al. 2005; G.L. Lacroix, unpublished data). The goal was to record multiple code transmissions during passage of a tagged fish even when several transmitters

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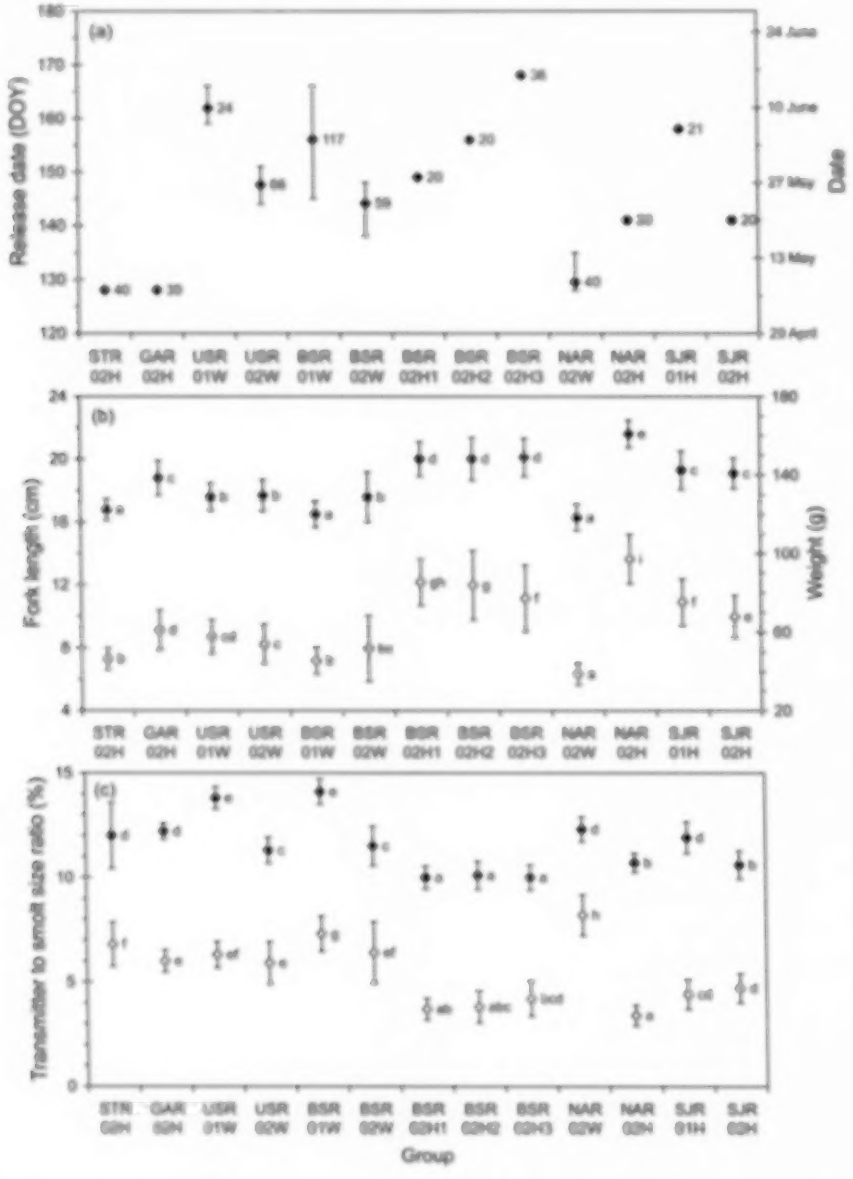
Fig. 2. (*a*) Timing of smolt tagging and release (date and mean day of year (DOY) ± range with number of smolts released shown), (*b*) fork length (solid diamonds) and weight (open diamonds), and (*c*) transmitter to smolt size ratio for length (solid diamonds) and weight (open diamonds) for Atlantic salmon (*Salmo salar*) from groups of different origin. Mean values (±SD in Figs. 2*b* and 2*c*) with different letters beside the bars are significantly different (ANOVA and Duncan's multiple range test, $p < 0.05$). Groups include river (STR, Stewiacke; GAR, Gaspereau; USR, Upper Salmon; BSR, Big Salmon; NAR, Nashwaak; SJR, Saint John), year (01, 2001; 02, 2002), origin (H, hatchery; W, wild), and hatchery release sequence (1, 2, 3).



were present. Mean distance between adjacent receivers in all arrays was 948 m (SD = 89.9 m, range = 600–1100 m) and mean water depth at monitoring sites was 99 m (SD = 44.4 m, range = 15–205 m). The first receiver in an array was <350 m from shore and distances between receivers were lowest nearshore because the observed range of detection was lower than offshore.

Receiver efficiency at detecting and identifying transmitters in the rivers and at the mouth of rivers was very high: it was 100% in tests conducted during the study at all sites monitored in rivers using transmitters from the same production batches as those used to tag salmon, and data from the study showed that 99.7% of tagged postsmolts monitored in the BoF ($n = 324$) were first successfully detected as smolts leaving the rivers. The efficiency of receiver arrays in marine habitat was also high: detection at the different arrays

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was 90%–100% in tests done at different times during the study by towing transmitters at a depth of 1–3 m across points along an array (both random points and the midpoint between adjacent receivers were tested), and data from the study showed that 88% (2001) and 94% (2002) of tagged postsmolts from inner BoF rivers monitored on the outer bay arrays were first successfully detected at the inner bay array, indicating that few tagged fish went by undetected at the inner bay array. Tests also showed that the efficiency of the outer bay array between Grand Manan Island and Nova Scotia (Fig. 1*b*) was probably higher than that of the inner bay array for several reasons. Tidal currents were generally not as severe, and some receivers were deployed near the bottom where reception was improved. In tests done with receivers at different depths, both percentage of transmissions recorded and maximum detection distance were greatest for receivers near the bottom. Finally, long sections of the array were set at an angle to the current thereby decreasing the effective distance between adjacent receivers and increasing the likelihood of detection if fish migrated with the current as observed by Lacroix et al. (2005).

Tracking systems (VR60-VH110/165) were also used, initially from the river banks and then on boats in estuaries and in the BoF, to search for transmitters that failed to exit a reach or an area bounded by receivers or arrays. When located, direction and rate of transmitter movement or lack thereof for an extended period were used to assign fate. This information was also used to supplement and verify data from receiver arrays. Data stored in monitoring receivers were downloaded at frequent intervals (1–2 weeks) where receivers were accessible from the surface; otherwise, this was done at intervals of 1–2 months and included receiver maintenance.

Treatment of telemetry data

Migration

The migration success of tagged salmon to the river mouth and to the inner and outer arrays in the BoF was calculated for each group from the numbers of tagged fish monitored at each location as a proportion of the tagged smolts leaving the release site near the head of tide. Calculations of migration success for the four groups migrating from the Saint John River estuary were adjusted to a common starting point at the confluence of the Saint John and Nashwaak rivers by deleting the few smolts that died upstream in each river (range = 0–3). Similarly, a few smolts that disappeared or died near release sites in other rivers (1.7% of smolts released) were excluded from the analysis.

Comparisons of migration success among groups of salmon monitored were done with a χ^2 analysis of association using observed frequencies (e.g., numbers of fish that passed and those available that did not pass at a monitoring site or array). The z ratio was used post hoc to assess the significance of the difference between two independent proportions for specific comparisons of migration success when χ^2 was significant for a comparison among several groups.

Distance travelled in a river and estuary was assumed to be the same for all smolts and excluded any back and forth movements with tides. In the BoF, mean distances were calculated for postsmolts from the direct line distance measured between the receivers at which each fish was first monitored. Passage times in different habitat segments monitored were calculated using the last record at one monitoring site (e.g., river mouth) and the first record at the next monitoring site (e.g., outer bay array). Maximum migration rate and speed (kilometres per day and body lengths per second to standardize for differences in length among groups) were calculated using distances for direct travel routes between two monitoring points. They excluded route searching behaviour or the effects of tidal currents on total distance travelled between these points (e.g., Lacroix et al. 2005). Mean values for these parameters were compared among groups using one-way analysis of variance (ANOVA) for independent samples and Duncan's multiple range test post hoc for multiple comparisons. The Pearson product–moment correlation coefficient (r) and t statistic were used to examine for correlation between parameters.

Fate and losses

The various monitoring arrays were used for a detailed attribution of tagged salmon losses to specific habitat segments based on known or assigned fate (dead or alive). In the Saint John River, the losses were tallied separately for the upper estuary (from the confluence of the Nashwaak and Saint John rivers to Evandale at the head of Long Reach and its confluence with Belleisle Bay) and lower estuary (from Evandale to Saint John Harbour Bridge at the river mouth) because of major changes in the river basin and salinity at that location (Fig. 1*a*) (Metcalfe et al. 1976). In other rivers, the segment monitored for losses was comparatively short and represented mostly estuarine habitat between the head of tide and river mouth. Monitoring in the Stewiacke River ended near its confluence with the Shubenacadie River and excluded 16 km of estuarine habitat leading to Minas Basin (Fig. 1*a*). Losses of postsmolts of inner BoF origin in the outer BoF segment were corrected by subtracting postsmolts not monitored at the outer bay array that were nevertheless monitored to be alive within the BoF more than a month after release. This assessment was based on the similarity of their movements to the resident behaviour previously identified for some postsmolts of inner BoF origin (Lacroix et al. 2005). Swimming speed was used also to ascertain that tagged postsmolts and not larger predators were monitored. Additionally, losses of postsmolts in 2001 were also attributed to coastal habitat near the mouth of the Big Salmon River, if they left that river but failed to migrate beyond a coastal array surrounding the river mouth, and to habitat within the Quoddy Region, if they were monitored entering but never leaving that region (Fig. 1*b*).

Survival estimates and models

Survival probabilities (S_i) of tagged salmon in each of the three main habitat segments bounded by monitoring arrays, estuaries (S_1), inner BoF (S_2), and outer BoF (S_3), were estimated using known or assigned fate. This approach, based on known-fate models (White and Burnham 1999), assumed that the monitoring probabilities (p_i) were 1.0 at each array bounding a habitat segment. This was accurate for estuarine survival ($p = 0.997$) but it probably underestimated marine survival ($p \approx 0.90$ based on tests previously described). However, the probability at each marine array would have

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been the same for all individuals. To account for resident postsmolts alive within a habitat segment, habitat-specific survival was calculated with the formula

$$S_i = (N_{i+1} + Nr_i)/N_i$$

where N_i is the number of tagged fish monitored entering habitat segment i, N_{i+1} is the number monitored leaving that segment at the next array, and Nr_i is the number of resident or nonmigrating fish not monitored leaving but found alive in the segment more than 1 month after release (i.e., after the last migrating fish in a group had left the BoF).

An information-theoretic approach (Burnham and Anderson 2002, 2004) was used to compare alternate models proposed to predict survival rate. This was based on Akaike's second-order information criterion (AIC_c), a statistic that can be used to identify the most parsimonious model by formally recognizing the trade-off between bias and variance (Burnham and Anderson 2002). A complex model with many parameters (K) will almost always fit the data better than a simpler model with few parameters (i.e., it will have a larger log-likelihood). However, parameter estimates from the complex model will be more uncertain. A model that fits well but has a minimum number of parameters is therefore preferred. When comparing a range of candidate models, the model with the lowest AIC_c value is considered to have the best out-of-sample predictive power based on the bias–variance trade-off. Models with similar AIC_c values relative to the best model (i.e., AIC_c difference = $AIC_i - AIC_{min} = \Delta_i = 0$–2) are considered to have strong support, whereas those with larger AIC_c differences are considered to have only moderate ($\Delta_i = 4$–7) or essentially no ($\Delta_i > 10$) support.

A set of 12 candidate linear models (g_i) was formulated a priori. In the first six models, parameters were incrementally added one at a time to assess their influence on the fate of individual fish (dead (0) or alive (1)). They included tag or tagging effect measured as transmitter length – smolt length (g_1), smolt fork length (g_2), migration or release date (g_3), rearing origin (g_4), year of migration (g_5), and natal or release watershed (g_6). The next six models were based on the hypothesis that reported differences in adult salmon returns to rivers of different regions of the BoF differ as a result of regional differences in survival rate during estuarine and early marine migration. The models included regions of origin (g_7) as constant parameters, with other parameters introduced to examine the following hypotheses: (*i*) hatchery rearing decreases fitness and survival compared with that of wild smolts (g_8), (*ii*) year of migration can have an important influence on survival because of differences in fitness or environmental conditions (g_9), (*iii*) marine survival increases with increasing smolt size (g_{10}), (*iv*) the timing of smolt migration or release varies among regions and can influence survival (g_{11}), and (*v*) there is an optimum time for migration or release and survival decreases if smolts are either early or delayed (g_{12}). The AIC_c differences were used to identify the best models. Akaike weights (w_i) provided a measure of the relative likelihood for each model in relation to the set of candidate models (i.e., probability on a scale of 1). When there was substantial evidence for several models, the relative importance of a model variable was estimated by summing the Akaike weights ($w_+(j)$) over all models that included the explanatory variable j. The best model identified for each of the migration strata was used to predict average habitat-specific survival.

The logit transformation was used as a link function to use survival data [0,1] in the linear regression models. Quantitative covariates (tag, fork length, release) were z-transformed (the value of the individual covariate was subtracted from the mean of that covariate for all individuals and divided by the standard deviation). Categorical variables (rearing, year) with two classification levels were treated as binary covariates in the regression and coded as follows: hatchery (0) and wild (1), 2001 (0), and 2002 (1). For other categorical groupings (five watersheds, three regions), the estimated mean survival values for the different groups (μ_i) were used as constants in the linear models. The models can thus be expressed as a general linear model:

$$\begin{aligned}\text{logit}(S_i) &= \log_e(S_i/(1 - S_i)) \\ &= \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \ldots + \beta_i X_i\end{aligned}$$

where β_0 is either a constant (μ_i) or the intercept, β_i is the slope of a regression, and X_i is a predictor variable.

Model parameters were estimated by maximizing the log-likelihood assuming that error in survival rates are binomially distributed using

$$S_i = \log_e[\text{binom}(S_g, 1)]$$

where S_i is the observed survival for an individual fish [0,1], and S_g is the predicted survival rate based on model g_i. Log-likelihood values were summed across all individuals, and parameters were adjusted using a nonlinear iterative search procedure until the summed log-likelihood was maximized (maximum likelihood estimate).

Results

Migration success, passage time, and migration rate

The overall migration success of Atlantic salmon to the outer boundary of the BoF differed among the 13 groups monitored ($\chi^2 = 80.15$, $p < 0.0001$, df = 12, $n = 224$) (Fig. 3). Those from intermediate inner BoF rivers on the New Brunswick coast usually had the highest success (range = 36%–70%), whereas those from distant inner BoF rivers in Minas Basin had the lowest success (3% and 8%, and significantly different from groups of intermediate inner BoF rivers ($\chi^2 = 109.84$, $p < 0.0001$, df = 8, $n = 188$)). Salmon from distant inner BoF rivers were relatively successful in leaving the rivers (88% and 72%) but not in reaching the inner bay array (10% and 21%) when compared with groups from the intermediate inner BoF rivers (range = 72%–91% to inner bay array and significantly different from groups of distant inner BoF rivers ($\chi^2 = 153.60$, $p < 0.0001$, df = 8, $n = 291$)). Few postsmolts from the Stewiacke and Gaspereau rivers were ever detected outside Minas Basin, either at monitoring arrays or during searches throughout the inner BoF.

Overall success was most consistent for groups from outer BoF rivers (range = 33%–45%; $\chi^2 = 4.81$, $p = 0.186$, df = 3, $n = 36$), but it was lower than for inner BoF groups from the same coast ($\chi^2 = 34.66$, $p = 0.0001$, df = 10, $n = 220$). This was partly a result of the consistently low success of smolts in leaving the Saint John River (range = 44%–59%; $\chi^2 =$

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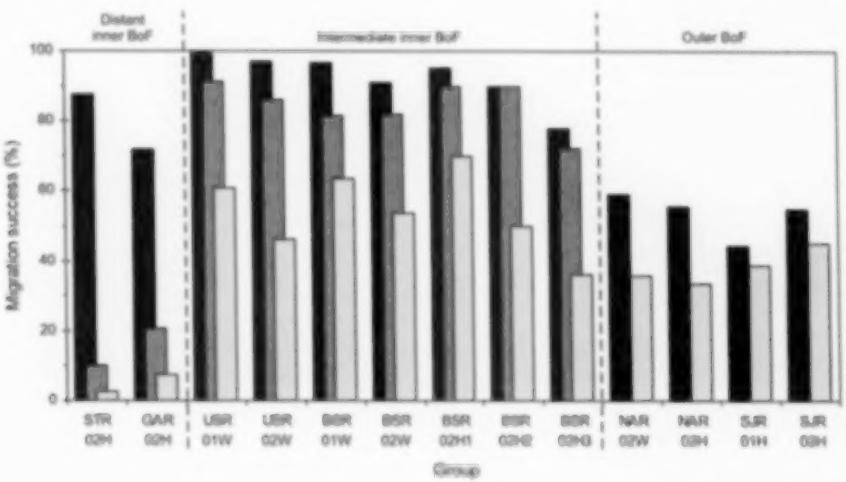
Fig. 3. Migration success of Atlantic salmon (*Salmo salar*) from groups of different origin to the river mouth (solid bars), the inner Bay of Fundy (BoF) array (dark shaded bars), and the outer BoF arrays (light shaded bars) as the percentage of tagged smolts entering the estuaries. Groups include river (STR, Stewiacke; GAR, Gaspereau; USR, Upper Salmon; BSR, Big Salmon; NAR, Nashwaak; SJR, Saint John), year (01, 2001; 02, 2002), origin (H, hatchery; W, wild), and hatchery release sequence (1, 2, 3). Groups are arranged by distance from the inner to outer BoF.



5.16, $p = 0.161$, df = 3, $n = 52$) compared with that of all groups leaving inner BoF rivers (range = 72%–100%; $\chi^2 = 207.99$, $p < 0.0001$, df = 12, $n = 428$).

For rivers where groups were monitored over 2 years (Upper Salmon River wild, Big Salmon River wild, and Saint John River hatchery groups), the migration success to different arrays did not differ significantly between years (z ratios, $p > 0.05$). Similarly, the migration success usually did not differ significantly between groups of wild and hatchery smolts for rivers where both were simultaneously monitored (Big Salmon and Nashwaak rivers in 2002) (z ratios, $p > 0.05$). However, in the Big Salmon River, the overall migration success of the last hatchery release was significantly lower than that of wild smolts (z ratio = 1.64, $p = 0.05$) and of hatchery smolts from the first release date (z ratio = 2.43, $p = 0.008$). There was a gradual decline in migration success from 70% to 36% with increasing release date for the hatchery groups in the Big Salmon River.

Migration distance for smolts in estuaries varied from <2 km in the steep gradient rivers on the New Brunswick coast of the inner BoF to >125 km in the Saint John River (Fig. 4). Nevertheless, passage time was relatively short for smolts moving down the Saint John River, as they migrated faster (range of means = 1.3–2.3 body lengths·s^{-1}) than smolts in other rivers (<0.35 body lengths·s^{-1}), covering mean distances of 23.4–38.2 km·day^{-1} compared with only 1.0–5.0 km·day^{-1} for all but one group in other rivers (Fig. 5). Passage time of smolts in the Stewiacke River was apparently delayed (mean = 13.6 days) compared with that in any of the other rivers (range of means = 0.15–6.6 days) considering that migration distance was <13 km to the estuary of the Shubenacadie River. Passage time and migration distance of smolts in estuaries were therefore not correlated ($r = 0.297$, $p > 0.05$).

Mean distances travelled by postsmolts in the BoF were <100 km for those leaving the Saint John River in the outer bay, 120–175 km for those from intermediate inner BoF rivers, and >230 km for those from distant inner BoF rivers. Passage time across the BoF was slow for postsmolts from inner BoF rivers, especially for those from distant rivers in Minas Basin (means = 25.6 and 34.6 days) compared with outer bay groups, some of which rapidly left the bay (range of means = 2.9–8.9 days for the three groups of large hatchery fish). In contrast, the small wild fish of outer BoF origin took as long to leave the bay (17.7 days) as both wild and hatchery groups from intermediate inner BoF rivers (range of means = 10.5–24.9 days). The large hatchery fish of outer BoF origin migrated faster in marine habitat (range of means = 0.9–2.0 body lengths·s^{-1} and 15.3–31.6 km·day^{-1}) than postsmolts of any other groups (range of means = 0.46–1.1 body lengths·s^{-1} and 8.0–17.0 km·day^{-1}). Interestingly, the marine migration rate of hatchery fish released at intervals in the Big Salmon River increased with delays in smolt release date, and mean passage time across the BoF decreased from 21.2 days for the first release to 10.5 days for the third release. Passage time and distance travelled by postsmolts in the BoF were correlated ($r = 0.891$, $p < 0.001$).

Habitat-specific losses

Losses of tagged salmon during migration were partitioned by habitat segment where fish were deemed to have died: estuary (upper and lower for Saint John River), coastal habitat close to river mouth (Big Salmon River in 2001, Stewiacke and Gaspereau rivers in 2002), inner BoF, Quoddy Region (in 2001), and outer BoF (Fig. 6). Losses for outer BoF groups were most important in the shorter, lower segment of the estuary, those for distant inner BoF groups occurred mostly inside the inner bay, and those for intermediate inner BoF groups were distributed among different habitats but increased in estuarine habitat with delays in release time of the hatchery groups.

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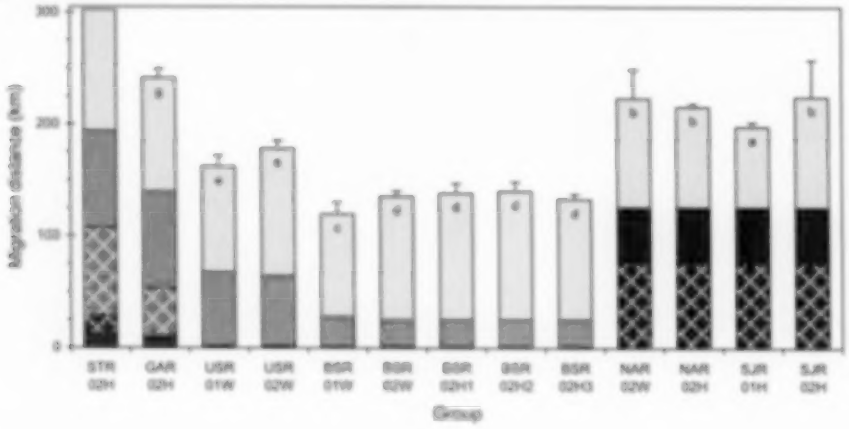
Fig. 4. Migration distance of Atlantic salmon (*Salmo salar*) from groups of different origin in different habitats: upper estuary (solid with cross-hatching, NAR and SJR), main estuary (solid), lower Shubenacadie River estuary (solid with cross-hatching, STR), Minas Basin (shading with cross-hatching, STR and GAR), inner Bay of Fundy (BoF) (dark shading), and outer BoF (light shading). Mean distances in the BoF (+SD) with different letters inside the bars are significantly different (ANOVA and Duncan's multiple range test, $p < 0.05$). Groups include river (STR, Stewiacke; GAR, Gaspereau; USR, Upper Salmon; BSR, Big Salmon; NAR, Nashwaak; SJR, Saint John), year (01, 2001; 02, 2002), origin (H, hatchery; W, wild), and hatchery release sequence (1, 2, 3).



The similarly high losses attributed to the inner bay for both rivers of the distant inner BoF region probably occurred in coastal habitat within Minas Basin, including the lower estuary of the Shubenacadie River for the Stewiacke River, based on the absence of transmitters from these groups in the inner bay segment. In contrast, losses when monitored in coastal habitat where the transition zone between the river mouth and the inner bay was short and open were found to be low (5 of 111 smolts exiting the Big Salmon River in 2001).

Few of the salmon losses in the outer bay occurred within the Quoddy Region when monitored in 2001. Only 2 of 10 postsmolts from intermediate inner BoF rivers monitored at the Quoddy arrays were never found again at arrays outside the Quoddy Region and may have died there. No postsmolts of outer BoF origin entered the Quoddy Region.

Estimated survival and evaluation of survival models

The estimated survival of smolts and postsmolts in different habitat segments provided further insight into the differences among groups monitored by taking into account migratory behaviour (Fig. 7). The survival of groups from intermediate inner BoF rivers in marine habitat was higher than initially indicated by the migration success because of the residency of some postsmolts (Fig. 3). This was most evident as the extent of residency increased with increasing release date for the hatchery groups in the Big Salmon River.

The survival models (g_1 to g_6) formulated to evaluate the relative importance of individual covariates indicated that transmitter length in relation to smolt length (i.e., tag effect), smolt length, release date, rearing origin, and year of migration were all considered unimportant in the three habitat strata when considered for the entire population monitored based on results of the AIC analysis (Table 1). The high AIC_c differences ($\Delta_i > 10$) and low Akaike weights (w_i) indicated that there was essentially no support for these models and that the variables were relatively unimportant predictors of survival. Adding watershed of origin (five categories) to the global model (g_7) only improved the model ranking to any extent for estuarine survival (based on Δ_i). Nesting the covariates within watershed categories did not improve the model likelihood for predicting survival in either the inner or outer BoF segments during migration.

The best predictive models were parsimonious and included region of origin (two or three categories) (Table 1). For estuarine survival (S_1), the region-rearing model (g_8) was the best, and the sum of Akaike weights for models with region was high (w_+(region) = 0.859), further indicating its importance as a predictive variable. This model predicted a higher survival for wild than for hatchery smolts (β = 0.783). There was also a substantial level of empirical support (Δ_i = 1.50) for a regional model with an optimum release period (g_{12}). Thus, model g_8 was only 2.1 times more likely to be the best model than model g_{12} (evidence ratio = 0.411/0.195) and reveals a certain amount of uncertainty regarding the best model. Model g_{12} predicted that survival gradually increased with increasing release date to an optimum period (DOY $\approx$ 140–150) and then decreased thereafter (S_1 = region μ_i – 0.317(release) – 0.316(release^2)). In contrast with these two models, there was considerably less support for the other proposed models.

The best model for survival in the inner BoF (S_2) was a regional model (g_{10}) with smolt length as an important variable predicting a slight increase in survival with increasing fork length (β = 0.334). There was also substantial support for a basic regional model (g_7) that predicted differences in postsmolt survival in the inner BoF between salmon migrating from distant and intermediate inner BoF rivers and for one that included rearing origin as a variable (g_9) that predicted a lower survival for wild than for hatchery smolts (β = –0.611). The sum of Akaike weights for these three highly likely regional models (w_+(region) = 0.757) indicates

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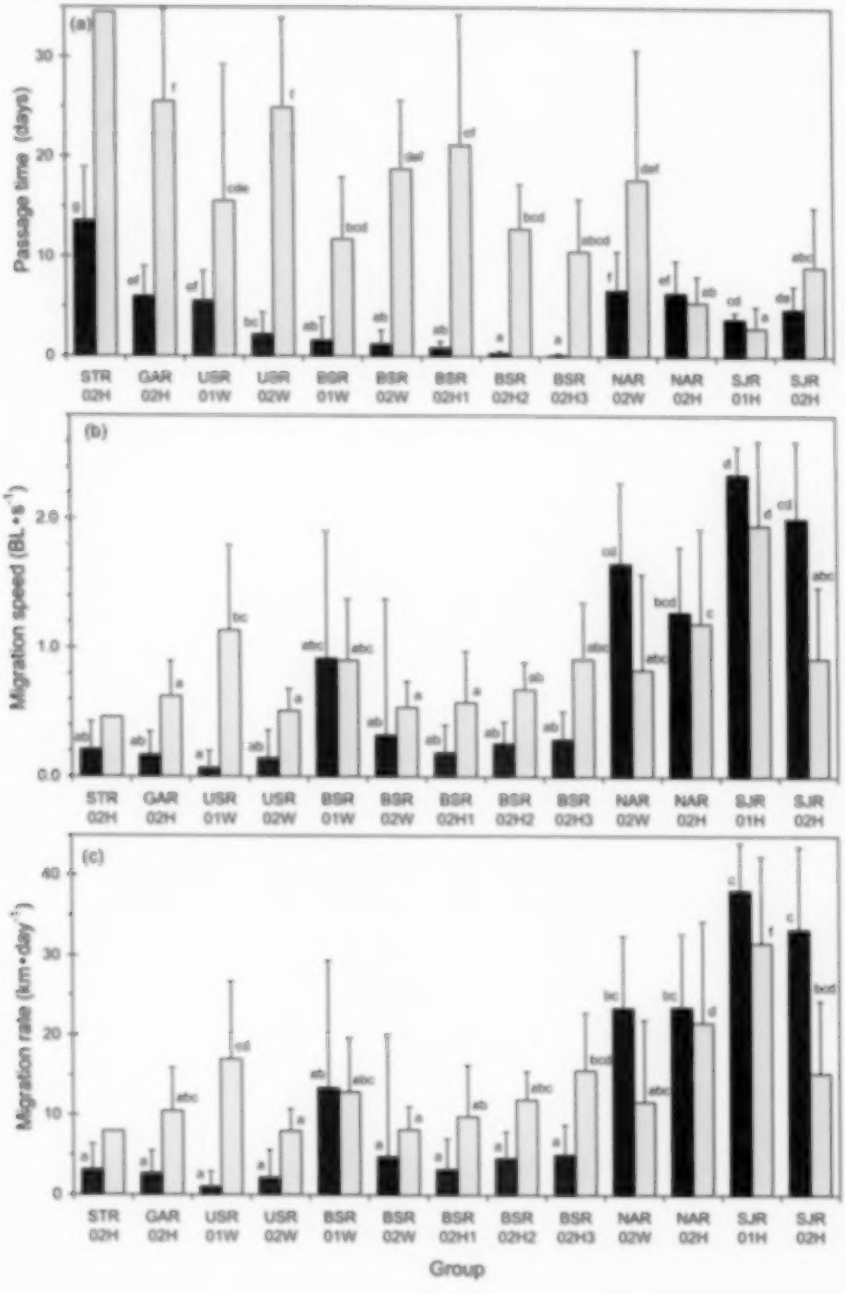
Fig. 5. (*a*) Passage time, (*b*) migration speed (BL, body lengths), and (*c*) migration rate of Atlantic salmon (*Salmo salar*) from groups of different origin in the estuaries (solid bars) and across the BoF (shaded bars). Mean values (+SD) with different letters above the bars are significantly different (ANOVA and Duncan's multiple range test, $p < 0.05$). Groups include river (STR, Stewiacke; GAR, Gaspereau; USR, Upper Salmon; BSR, Big Salmon; NAR, Nashwaak; SJR, Saint John), year (01, 2001; 02, 2002), origin (H, hatchery; W, wild), and hatchery release sequence (1, 2, 3).



that region of origin was the most important predictive variable for survival in the inner BoF segment.

Survival in the outer BoF (S_3) was best predicted by a regional model (g_8) that included year of migration as a variable. This model with a high Akaike weight (w_i = 0.605) predicted differences among the regions of origin and a lower survival of postsmolts in 2002 compared with 2001 (β = –0.998). The importance of year of migration as a var-

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Fig. 6. Proportion of total losses (number shown inside the bars) of Atlantic salmon (*Salmo salar*) from groups of different origin attributed to different habitats: upper estuary (solid with cross-hatching), main estuary (solid), coast near the river mouth (dark shading with cross-hatching), inner Bay of Fundy (BoF) (dark shading), Quoddy Region (light shading with cross-hatching), and outer BoF (light shading). Groups include river (STR, Stewiacke; GAR, Gaspereau; USR, Upper Salmon; BSR, Big Salmon; NAR, Nashwaak; SJR, Saint John), year (01, 2001; 02, 2002), origin (H, hatchery; W, wild), and hatchery release sequence (1, 2, 3).

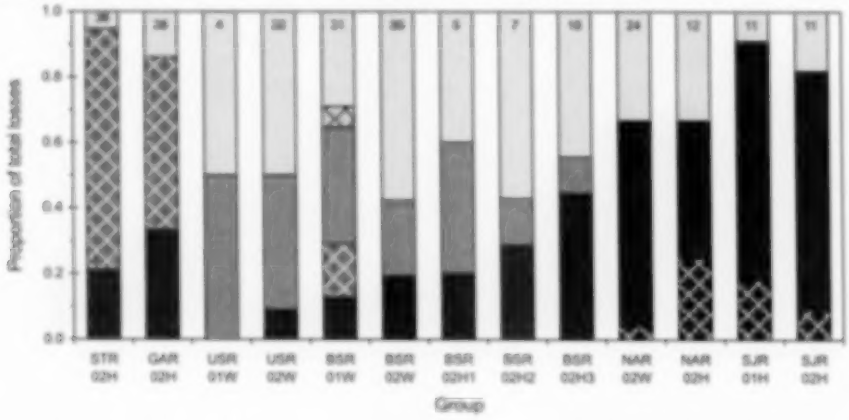
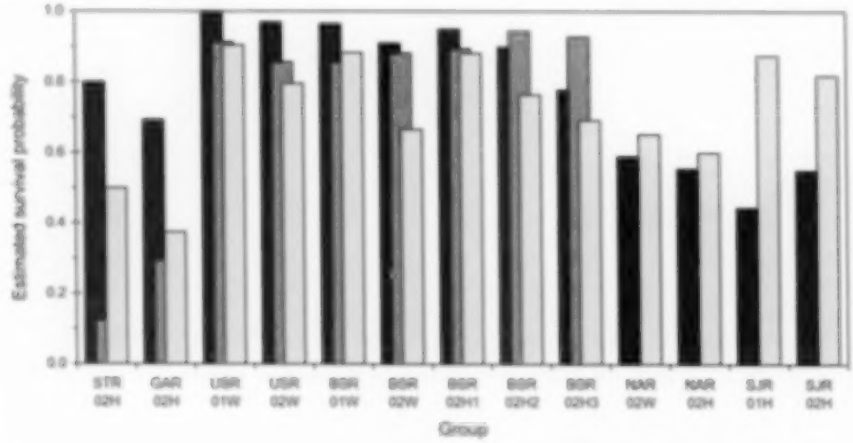


Fig. 7. Estimated survival probability (S_i) of Atlantic salmon (*Salmo salar*) from groups of different origin within the estuaries (solid bars), the inner Bay of Fundy (BoF) (dark shaded bars), and the outer BoF (light shaded bars). Groups include river (STR, Stewiacke; GAR, Gaspereau; USR, Upper Salmon; BSR, Big Salmon; NAR, Nashwaak; SJR, Saint John), year (01, 2001; 02, 2002), origin (H, hatchery; W, wild), and hatchery release sequence (1, 2, 3).



iable was also reflected by its inclusion in the next-best model (g_8) (Δ_i = 2.54) and by its sum of weights (w_+(year) = 0.775) compared with that for region (w_+(region) = 0.696). All other models considered had comparatively high AIC_c values and considerably less support ($\Delta_i > 4$).

The best model in each habitat segment was used to predict the average survival of salmon migrating from each region and highlight the differences among regions (Table 2). The survival was predicted to be consistently high in all habitats for salmon from the intermediate inner BoF region. Predicted survival of smolts was 1.7 times higher in the estuaries of the intermediate inner BoF region than in the estuary of the outer BoF region. Predicted survival of postsmolts migrating from the intermediate inner BoF region was 4.3 times higher in the inner BoF segment and 1.9 times higher in the outer BoF segment than that of salmon from the distant inner BoF region. As a result, salmon from the intermediate inner BoF region had the best predicted overall survival by a large margin over the rate for the other regions. The predicted overall survival rate of salmon from the distant inner BoF region was minimal and indicated that adult returns after 1 year at sea were unlikely.

Discussion

The early marine survival of migrating Atlantic salmon was estimated by monitoring their migration in estuarine and coastal habitats. As a result, specific hypotheses put forth for the decline of salmon populations were evaluated both generally and specifically for the endangered salmon in the BoF (inner BoF populations) (Committee on the Sta-

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Table 1. Akaike's second-order information criterion (AIC_c) of the regression models of Atlantic salmon (*Salmo salar*) survival (S_i) in different habitat segments during migration from the Bay of Fundy (BoF).

Model	Predictor variable(s)	log(L)	K	AIC_c	Δ_i	w_i
S_1: estuaries (n_1 = 509)						
g_1	Tag	−225.05	2	454.13	69.56	0.000
g_2	Tag, FL	−224.64	3	455.32	70.75	0.000
g_3	Tag, FL, release	−213.35	4	434.78	50.21	0.000
g_4	Tag, FL, release, rearing	−208.93	5	427.99	43.41	0.000
g_5	Tag, FL, release, rearing, year	−207.70	6	427.57	43.00	0.000
g_6	Tag, FL, release, rearing, year, watershed	−183.62	10	387.69	3.11	0.087
g_7	Region	−191.29	3	388.62	4.05	0.054
g_8	**Region, rearing**	**−188.25**	**4**	**384.57**	**0.00**	**0.411**
g_9	Region, year	−190.68	4	389.43	4.86	0.036
g_{10}	Region, FL	−189.41	4	386.90	2.32	0.129
g_{11}	Region, release	−189.79	4	387.65	3.08	0.088
g_{12}	Region, release, release^2	−187.98	5	386.07	1.50	0.195
S_2: inner BoF (n_2 = 372)						
g_1	Tag	−199.82	2	403.68	110.00	0.000
g_2	Tag, FL	−197.62	3	401.31	107.62	0.000
g_3	Tag, FL, release	−154.45	4	317.02	23.33	0.000
g_4	Tag, FL, release, rearing	−148.98	5	308.11	14.43	0.000
g_5	Tag, FL, release, rearing, year	−148.55	6	309.34	15.65	0.000
g_6	Tag, FL, release, rearing, year, watershed	−142.43	9	303.37	9.68	0.003
g_7	Region	−145.52	2	295.07	1.39	0.197
g_8	Region, rearing	−144.68	3	295.43	1.75	0.165
g_9	Region, year	−145.34	3	296.74	3.06	0.086
g_{10}	**Region, FL**	**−143.81**	**3**	**293.68**	**0.00**	**0.395**
g_{11}	Region, release	−145.21	3	296.48	2.79	0.098
g_{12}	Region, release, release^2	−144.73	4	297.58	3.89	0.056
S_3: outer BoF (n_3 = 339)						
g_1	Tag	−177.27	2	358.58	12.29	0.001
g_2	Tag, FL	−175.83	3	357.74	11.46	0.002
g_3	Tag, FL, release	−171.22	4	350.56	4.27	0.071
g_4	Tag, FL, release, rearing	−170.51	5	351.19	4.91	0.052
g_5	Tag, FL, release, rearing, year	−169.29	6	348.83	2.54	0.170
g_6	Tag, FL, release, rearing, year, watershed	−167.20	10	355.07	8.78	0.007
g_7	Region	−174.18	3	354.44	8.15	0.010
g_8	Region, rearing	−174.13	4	356.37	10.09	0.004
g_9	**Region, year**	**−169.08**	**4**	**346.28**	**0.00**	**0.605**
g_{10}	Region, FL	−174.06	4	356.24	9.96	0.004
g_{11}	Region, release	−171.79	4	351.71	5.43	0.040
g_{12}	Region, release, release^2	−170.95	5	352.09	5.80	0.033

Note: The log-likelihood (log(L)), number of parameters (K), AIC_c differences (Δ_i), and Akaike weights (w_i) are listed for each candidate model (g_i), and the number of observations (n_i) retained for analysis in each habitat segment is shown. The model with the minimum AIC_c is shown in bold. Model covariates and categorical variables are tag (transmitter length / smolt length), FL (smolt fork length), release (smolt migration or release date), rearing (wild versus hatchery origin), year (2001 versus 2002 migration), watershed (five levels), and region (two or three levels).

Table 2. Model predictions of survival rate (S_i) for Atlantic salmon (*Salmo salar*) from different regions of the Bay of Fundy (BoF) in estuaries (S_1), the inner BoF (S_2), and the outer BoF (S_3) and predicted overall survival ($S_O = S_1 \times S_2 \times S_3$).

Region	S_1	S_2	S_3	S_O
Inner BoF (distant)	0.7468	0.2065	0.4167	0.0643
Inner BoF (intermediate)	0.9349	0.8790	0.8059	0.6623
Outer BoF	0.5446	na	0.7207	0.3959

Note: na, not applicable for that region.

tus of Endangered Wildlife in Canada 2006). This was the first large-scale study in marine habitat to test the premise that electronic tagging of migrating fish and automated monitoring with a succession of long arrays of underwater receivers or "curtains" to intercept transmitters at interval across the migration route could provide accurate, direct measures of migration success in different strata to estimate habitat-specific survival.

Previous attempts at estimating early marine survival of salmon have been based on exploitation rates in fisheries during the first year at sea (e.g., Kallio-Nyberg et al. 2004; Saloniemi et al. 2004); otherwise, estimates of marine sur-

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vival have been based on smolt-to-adult estimates in rivers and encompassed the entire marine phase. The present study focussed on a specific portion of the marine period during which determinations of migration success were very accurate compared with those by the above methods. The high probability of detection of tagged salmon, identification of areas where losses occurred, and inclusion of behaviour all contributed to the accuracy of habitat-specific survival estimates. Nevertheless, estimates of survival in marine habitat were deemed to be minimum estimates ($p_i < 1.0$), thereby reducing the probability of not rejecting some null hypothesis about factors affecting survival (type II error).

The overall migration success of salmon from the BoF generally varied little among groups within a watershed or region of origin compared with the scale of differences among the three regions monitored. Salmon from the intermediate inner BoF region (endangered populations from Upper Salmon and Big Salmon rivers) had the highest migration success and initially fared better than those from the outer BoF region. In contrast, few salmon from the distant inner BoF region (endangered populations from Stewiacke and Gaspereau rivers in Minas Basin) survived to emigrate from the head of the BoF. The low variation in migration success among groups within each region compared with the variation among regions indicated that different specific regional factors rather than factors common to the BoF as a whole were probably responsible.

This initial assessment was supported by the AIC evaluation of regression models for estimated survival. It indicated that the most important variable accounting for differences in survival of migrating salmon in all three habitat strata monitored was region of origin, a categorical criterion rather than an individual covariate. The best models were those that also included other explanatory variables within regions, and these differed among the different habitat segments. They were rearing origin and the timing of migration or release for estuarine survival, rearing and smolt size for survival in the inner BoF area, and year of migration for survival in the outer BoF segment. The analysis indicated that transmitters (i.e., size-related effect of transmitters) and tagging, smolt size, migration or release date, rearing origin, or year of migration did not explain differences in survival in any habitats when looking at the entire population tagged and monitored. There was substantial support only for models constrained by a geographic component.

Regional influence was further emphasized by differences in habitats where salmon losses occurred. The high losses of smolts in the lower estuary of the Saint John River greatly affected the overall success of salmon migrating from that region compared with smolt losses in the other two regions. The high losses of postsmolts in Minas Basin as they left the Stewiacke and Gaspereau rivers accounted for the very low migration success of salmon from the distant inner BoF region. In contrast, there was no one specific habitat where losses were concentrated for salmon from the intermediate inner BoF region. These regional differences further indicated that no single factor or habitat controlled the survival and emigration of salmon from rivers of the BoF. Factors potentially affecting salmon survival in different habitat strata were therefore examined taking into account these regional differences.

The collapse of salmon populations from rivers throughout the inner BoF area has been hypothesized to be related to a lower early marine survival of postsmolts within the BoF compared with populations from major rivers in the outer BoF area (Cairns 2001). The very low survival of salmon from the distant inner BoF region in coastal habitat, especially in Minas Basin inside the inner BoF area, provided support for this premise. However, it was not supported by the evidence for salmon from the intermediate inner BoF region where the estimated early marine survival of postsmolts in the BoF was higher than that estimated for postsmolts from the outer BoF region. The similarity in predicted postsmolt survival in the outer BoF area for salmon from the intermediate inner BoF and outer BoF regions indicated that major differences in survival must be occurring later in the marine period to account for the failure of adult salmon to return to the Upper Salmon and Big Salmon rivers compared with returns to the Saint John River system (Amiro 2003; Gibson et al. 2003; Jones et al. 2006).

The potential importance of low survival of smolts in estuarine habitat in controlling adult returns has generally been disregarded, while the blame is placed on early marine mortality. Yet, estimated survival was much lower for smolts in the Saint John River estuary than for postsmolts in the BoF, indicating that smolt losses could have a strong influence on adult returns in some rivers with extensive estuarine habitat. These losses occurred mostly in reaches of the lower estuary, with bottlenecks where potential predators aggregated. These included double-crested cormorant (*Phalacrocorax auritus*) (Blackwell et al. 1997), harbour seal (*Phoca vitulina*) (Browne and Terhune 2003), and striped bass (*Morone saxatilis*) (Blackwell and Juanes 1998; Beland et al. 2001) that were probably attracted by the abundance of anadromous alewife (*Alosa pseudoharengus*) and American shad (*Alosa sapidissima*) entering the river during spawning runs in April and May. Stationary transmitters from smolts that failed to leave the river were found in areas of the lower estuary where these potential predators aggregated.

The estuarine survival of smolts was very high in rivers of the intermediate inner BoF region compared with the other regions. These steep-gradient rivers, typical of that area of the New Brunswick coast, had very short estuaries (<2 km) that drained directly into the BoF in an area with few coves and swept by extreme tidal currents. These features greatly reduced available habitat for potential predators in the estuaries and along the coast. The low losses in the area just outside the river mouth for groups from the Big Salmon River and the low losses inside the inner bay for groups from both the Upper Salmon and Big Salmon rivers indicated that the impact of predators was relatively low in habitat along that stretch of the New Brunswick coast where postsmolts are known to migrate close to shore (Lacroix et al. 2005). They also showed that the transition to salt water in the BoF was initially successful even though it occurred rapidly compared with systems with longer estuaries. Lacroix et al. (2005) found that the majority of smolts from the Big Salmon River entered the BoF on an ebb tide soon after high water and rapidly left the coastal area (92%–100% survival within 10 km of the river mouth), reducing risk from avian predators seen aggregating at the mouth of the river and on tidal flats at low tide.

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In contrast, the period of migration from the river as salmon entered coastal habitat was critical for populations in rivers of the distant inner BoF region. Survival probabilities of 0.75 for smolts and 0.21 for postsmolts during the period of transition to marine habitat in Minas Basin would greatly limit recruitment. This could lead to population failure if the situation persisted over more than several generations. The collapse of the salmon populations in these inner BoF rivers occurred in three generations and <15 years (Amiro 2003; Irvine et al. 2005). There are several hypotheses for this very low survival of migrating salmon before they apparently reached open waters of the BoF: (*i*) a potentially high impact of predators in estuarine and coastal habitats of Minas Basin, (*ii*) a possible disruption of smolting physiology and behaviour related to hatchery rearing or release date and delayed migration, and (*iii*) a potential for by-catch in the Atlantic herring (*Clupea harengus*) fishery of Scots Bay in Minas Channel.

The native striped bass population in the Shubenacadie River – Grand Lake system of Minas Basin was estimated at 18 000–27 000 in 2002, at least 15 000 of which were of minimum reproductive age (≥3 years) (Douglas et al. 2003). These large bass (>35 cm) descended from the lake to the estuary en masse in the spring (2–24 May) and entered the lower Stewiacke River to spawn. The absence of recaptures outside of Minas Basin from 2500 adult striped bass marked on the Shubenacadie River indicated the probable extent of their range (Douglas et al. 2003). This abundance of striped bass, including immature ones, and habitat overlap with emigrating salmon would have increased the probability of salmon predation. Predation of salmon smolts by immature striped bass was observed by Beland et al. (2001). An unknown number of nonnative striped bass originating from rivers of the United States also enter Minas Basin and its estuaries during spring (Wirgin et al. 1995), and they would have added further to the potential predation of postsmolts. There were very high densities of both immature and mature herring in Scots Bay at the mouth of Minas Basin and distributed throughout Minas Channel in the summer of 2002 (Melvin et al. 2003). Herring are prominent in the diet of many fish, birds, and marine mammals, and their abundance would have attracted predators and further increased the possibility of opportunistic predation on postsmolts migrating through Minas Channel at the same time.

Hatchery-reared smolts were released early (8 May) in rivers of the distant inner BoF region compared with wild smolt runs based on a mid-May to mid-June migration in the Stewiacke River (Amiro and Jefferson 1996). A lack of readiness to migrate could have accounted for their slowness in leaving the rivers (mean delays of 6 and 14 days in the Gaspereau and Stewiacke rivers, respectively). These delays could then have affected smolts and especially postsmolts upon entry into Minas Basin if the physiology and behaviour associated with smolting had been disrupted. Migration delays beyond the normal smolting time associated with warm or increasing water temperature exceeding a degree-days threshold can lead to the loss of smolt characteristics and have a negative impact on survival (McCormick et al. 1999; Zydlewski et al. 2005). Water temperature decreased slightly and was usually <10 °C in the first 2 weeks after smolt release in both rivers; it then increased over the next 2 weeks and decreased again by mid-June (G.L. Lacroix, unpublished data). The increase in water temperature was greatest in the Stewiacke River, and cumulative degree-days between smolt release and mid-June were greater in the Stewiacke River (554) than in the Gaspereau River (470). However, these differences did not lead to significant differences in postsmolt mortality between rivers, and a negative impact of temperature on smolting and survival is questionable in this case. A comparison with wild smolts, while desirable, was impossible because they were too rare to allow tagging (Amiro 2003).

The slow migration rates observed for smolts and postsmolts from the rivers of Minas Basin meant that some postsmolts could have been leaving the basin near the end of June, increasing the likelihood of overlap with the start of the herring fishery and of by-catch. One of the largest purse-seine fisheries for herring with some of the highest catch levels in the management zone occurred during July–September of 2002 on the Scots Bay spawning grounds at the mouth of Minas Basin (Power et al. 2003). This fishery extended right across Minas Channel and the migration path of salmon leaving Minas Basin.

A comparison between salmon of wild and hatchery origins was possible in the Big Salmon River. Rearing was an important component of the regional survival models in estuaries and the inner BoF area. Smolt survival was predicted to decrease for hatchery groups if their migration was delayed (i.e., experimental late release date). This was also reflected in the next best survival model with evidence for an optimal smolt migration time where smolt survival decreased when smolts were delayed beyond that time. This was especially evident for the hatchery release 20 days after the last wild smolt was tagged. Their physiology may have been adversely affected by the delay beyond normal migration dates because of the impact that cumulative temperature in freshwater can have on smolting (McCormick et al. 1999; Zydlewski et al. 2005). In contrast, postsmolt survival in the inner BoF area was predicted to increase for delayed hatchery groups, as they migrated through the area much more rapidly than other earlier groups. It has been suggested that hatchery rearing will decrease marine survival and affect adult return rates but that this can be partially overcome by the larger size of hatchery smolts and a size-related increase in marine survival (Ritter 1989; Kallio-Nyberg et al. 2004; Saloniemi et al. 2004). The best survival model for the inner BoF area indicated that, regionally, smolt length was an important variable. There was an increase in estimated survival for the larger hatchery fish from the Big Salmon River. Interestingly, this contrasted with a decrease in overall migration success from the BoF for the same large hatchery smolts with delayed release. The paradox can be explained by an increase in residency rate for these hatchery fish released late. This nonmigratory behaviour was also observed by Lacroix et al. (2005) for this salmon population. A similar behaviour has been reported for Atlantic salmon in the Baltic Sea (Salminen et al. 1994).

The responses of hatchery fish to delays in release indicated that synchronizing the readiness and release time of hatchery smolts to the timing of wild smolt runs may be crucial to successful management of the depleted or endangered salmon populations being sustained by hatchery programs in

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the BoF. The models for estuarine survival indicated that timing of hatchery releases was a more important explanatory variable than smolt size, probably because of the control that cumulative temperature has on smolting and survival. For example, the smallest wild smolts and the largest hatchery smolts in the study (both from the Nashwaak River) had similar estuarine and marine survival probabilities, indicating that the release of hatchery smolts several weeks later than wild smolts may have negated their size advantage.

Models for survival in the outer BoF area did not reveal any of the influence of rearing, smolt size, or migration date on survival seen for models in other habitat strata. Differences were regionally based and there was usually a lower survival of postsmolts in the outer BoF area in 2002 than in 2001. This difference could have been due to annual differences in probability of transmitter detection at the outer BoF array because of differences in efficiency, but it may also be a function of the different location of the array in 2002 and an increase in migration distance. This increase was reflected in the significantly longer passage time through the outer BoF area in 2002 than in 2001, increasing exposure to factors potentially affecting survival. The following factors were evaluated in relation to the losses of postsmolts that occurred in the outer BoF area: (*i*) migratory behaviour, (*ii*) potential interaction with Atlantic salmon farms, (*iii*) potential by-catch in various fisheries, (*iv*) habitat suitability, and (*v*) predation.

Predicted average survival in the outer BoF area was highest for postsmolts from the intermediate inner BoF region regardless of their late migration date and slow migration rate compared with that of fish from the outer BoF region. Although estimated postsmolt survival in the outer BoF did decrease slightly with increasing delay in release of hatchery groups in the Big Salmon River, their survival remained high and comparable with that of wild fish. The slow passage time of postsmolts from the inner BoF was a function of migration distance, but it was also increased by the delaying effects of extreme tides in the inner BoF (Lacroix et al. 2005). These differences in migratory behaviour between postsmolts from the inner and outer BoF regions had a number of implications with other factors potentially affecting survival.

Delays in release and slow passage time not only extended the presence of postsmolts in the BoF, but also apparently increased the extent of nonmigratory behaviour for fish from the inner BoF region. A large proportion of postsmolts of inner BoF origin returned to or remained in the BoF over the summer (range = 29%–90% of postsmolts alive from different groups; G.L. Lacroix, unpublished data). Jessop (1976) first reported captures of postsmolts of inner BoF origin in the BoF throughout the summer, and Lacroix et al. (2005) previously measured a high residency of postsmolts from the Big Salmon River over the summer. These postsmolts would be exposed to coastal factors that would not affect postsmolts from the outer BoF region, which rapidly left the BoF and are known to migrate to feeding grounds off Newfoundland and in the Labrador Sea area west of Greenland (Montevecchi et al. 1988; Ritter 1989).

The effect of tides and the long passage time of postsmolts from inner BoF rivers increased their dispersal throughout the BoF, but only a few of these postsmolts ended up in the Quoddy Region where salmon farms were concentrated. Postsmolts from the Saint John River left the bay rapidly and directly without entering the area. Therefore, interaction of postsmolts with salmon farms of the Quoddy Region was probably not a factor affecting early survival in the outer BoF area. Potential impacts of migration near these farms could have included predation from aggregations of predators around farms and the transmission of diseases and parasites (Department of Fisheries and Oceans 1999; Lacroix et al. 2004*b*). Lacroix and Knox (2005) found that there was a possibility of postsmolt contact with salmon farms concentrated along the east coast of Grand Manan Island during migration, but this area was beyond the outer BoF array.

The slow departure and residency of postsmolts from the inner BoF region could have increased the possibility of by-catch in several fisheries during the summer. There is some evidence of postsmolt by-catch in the herring fishery that uses fixed weirs in the BoF (Jessop 1976; Lacroix et al. 2004*b*). This fishery, concentrated in the Quoddy Region, on the east coast of Grand Manan Island, and along the southern coast of Nova Scotia, generally occurs in July–August (Power et al. 2003). As a result, postsmolts of inner BoF origin with a slow passage time and wide dispersal through the outer BoF have more commonly been found in weirs during the first summer at sea (Jessop 1976). Lacroix and Knox (2005) found that there was a potential for postsmolt by-catch in the extensive pelagic fishery in the outer BoF and northern Gulf of Maine based on the spatial and temporal overlap between the distribution of migrating postsmolts and commercial catches of herring and the strong association between the two species during research surveys (e.g., herring were captured at 80% of sites with postsmolts). The possibility of by-catch would have been high for postsmolts from the inner BoF region that migrated later or were resident at a time when herring catches by the purse-seine fishery were high off the east coast of Grand Manan Island and along the coast of Nova Scotia at the level of the outermost monitoring array (Power et al. 2003). A similar potential for significant by-catch of migrating postsmolts by an extensive surface trawl fishery for mackerel has been identified in the Norwegian Sea (Holm et al. 2003).

Differences in migration timing and behaviour between postsmolts of different regions meant that they experienced different conditions as water temperature increased from about 6 °C in early May when fish from the outer BoF region started leaving to 12 °C in late July when those from the inner BoF region were monitored (based on measurements across the monitoring arrays; G.L. Lacroix, unpublished data). Low sea surface temperature during the early phase of marine migration is considered to affect growth and survival during the postsmolt year and to influence recruitment in Atlantic salmon (Friedland et al. 2000, 2005). However, the temperature range for these effects is not always clear. Surface temperature in the BoF was relatively uniform and increasing during migration and was unlikely to result in major immediate differences in survival of postsmolts among regions. Satellite measurements of

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ocean temperature (available from www.gomoos.org) confirmed that surface temperature was within a range that favoured postsmolt growth and survival throughout most of the BoF during migration. Lacroix and Knox (2005) found postsmolts of different origins in the outer BoF area to have started feeding on pelagic prey (i.e., amphipods, euphausiids, and fish larvae) abundant in that area. Also, circuli spacing on scales indicated that the accelerated marine growth phase had started while postsmolts were still in the BoF.

Many potential salmon predators occur in the highly productive outer part of the BoF and take advantage of seasonally abundant pelagic prey (Ritter 1989). Atlantic salmon postsmolts generally migrate near the surface (Holm et al. 2003; Lacroix and Knox 2005), which would make them easy prey. During the study, cormorants, ospreys (*Pandion haliaetus*), gannets (*Morus* spp.), harbour seals, grey seals (*Halichoerus grypus*), and schools of Atlantic white-sided dolphin (*Lagenorhynchus acutus*) were some of the potential predators seen feeding in areas of the outer BoF where postsmolts migrated. However, evidence of predation on salmon is usually circumstantial and difficult to obtain (see reviews by Middlemas et al. (2003) and Montevecchi and Cairns (2003)). The late migration of postsmolts from the inner BoF region coincided with high densities of herring in the outer BoF reported by Power et al. (2003), which would have attracted predators. Lacroix and Knox (2005) found postsmolts to be frequently associated with other pelagic prey such as alewife, herring, and Atlantic mackerel (*Scomber scombrus*). They also found a strong association between spiny dogfish (*Squalus acanthias*), a potential predator, and postsmolts; dogfish occurred at 22% of sites in the outer BoF where postsmolts were caught in a 2001 survey, and almost all samples with dogfish also had postsmolts. Therefore, it seems that the opportunities for predation would be high while postsmolts remained in the BoF.

Predicted overall survival in the BoF indicated that there would probably be no returns of adult salmon to the rivers of the distant inner BoF region. However, returns of adult salmon would have been expected in rivers of the other two regions based on predicted initial survival from the BoF. The smolt-to-adult return rates for the two cohorts monitored in this study were very low for the outer BoF rivers (0.45%–0.60% for Saint John River hatchery origin and 3.2% for Nashwaak River wild origin), but returns to the rivers of the intermediate inner BoF region were almost nonexistent (Jones et al. 2006). Although this could be related to differences in survival rate later in the marine phase, it was probably also a function of the low numbers of smolts leaving these inner BoF rivers in 2001 and 2002 (Flanagan et al. 2006).

Differences in survival rate between salmon from the inner and outer BoF regions were expected to occur later on if they exploited different marine habitats as a result of differences in migratory behaviour. One hypothesis to explain differences in the status of salmon populations in different regions of the BoF is that postsmolts that migrated rapidly offshore would be more likely to return as adults, whereas those that remained in or near the BoF would be affected by a decrease in survival rate related to various factors in coastal habitat. A similar extended residence of some salmon postsmolts was reported in a distant region of the Baltic Sea, possibly in response to the large size of hatchery smolt and food availability (Salminen et al. 1994; Kallio-Nyberg et al. 1999). Saloniemi et al. (2004) found that extensive stocking of hatchery smolts used to counteract the decline in salmon abundance in the Baltic Sea has had limited success because of a lower marine survival of hatchery smolts than of wild smolts, regardless of their large size. They questioned whether endangered wild salmon populations could be effectively enhanced by simply stocking greater numbers of bigger fish. The recovery strategy for endangered salmon populations in the inner BoF region is based on a captive breeding program and extensive stocking of hatchery-reared juveniles of inner bay lineage (Gibson et al. 2004; Flanagan et al. 2006). The success of this strategy for recovery and conservation could ultimately depend on factors that influence or modify the migratory behaviour and survival of these reared fish if survival rates in coastal habitat of the BoF and in marine habitat of the Northwest Atlantic differ markedly. Although poor early marine survival associated with an apparent predator problem could have caused the failure of the populations in rivers of Minas Basin in the years monitored, it was not considered to be limiting the return of salmon to rivers of the intermediate inner BoF region. Factors outside the period and (or) region monitored in this study must therefore be considered for the failure of those endangered salmon populations.

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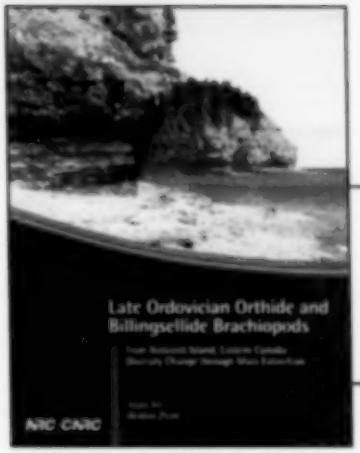
from Anticosti Island, Eastern Canada: Diversity Change Through a Mass Extinction



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Jisuo Jin and Renbin Zhan

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This monographic study deals with a major marine faunal turnover during the Late Ordovician global greenhouse/icehouse episodes. The Late Ordovician was marked by one of the two greatest global sea-level rises and inundations of the North American paleocontinent during the Phanerozoic (last 544 million years), accompanied by a rapid diversification of invertebrate faunas in shallow, tropical, epicontinental seas. Toward the end of the Late Ordovician, continental glaciation in the southern hemisphere (Gondwana landmass) caused a major sea-level drop and marine regression from North America, bringing about the first of the five major mass extinction events in life history. Anticosti Island was part of the larger Anticosti basin, located on the eastern continental shelf of the North America paleocontinent, and was covered by a shallow, tropical sea in the Late Ordovician epoch. During the latest Ordovician global mass extinction event, the marine shelly benthos (bottom) of the Anticosti basin experienced a significant local radiation. This provides a great opportunity for us to investigate the response of marine life to a major environmental crisis. This monographic study aims to document the diversity change of brachiopods (one of the major groups of marine life during the Ordovician Period) from pre-extinction to extinction times.

Cette étude monographique porte sur un renouvèlement majeur de la faune marine survenu à la suite d'épisodes planétaires d'effet de refroidissement et de réchauffement lors de l'Ordovicien tardif. Cette période a d'ailleurs été marquée par l'une des deux plus importantes élévations du niveau de la mer mondial et inondations du paléocontinent nord-américain du Phanérozoïque (les 544 derniers millions d'années). Ce bouleversement a aussi été accompagné par une diversification rapide de la faune d'invertébrés dans les mers épicontinentales tropicales et peu profondes. Vers la fin de l'Ordovicien tardif, la glaciation continentale dans l'hémisphère méridional (masse terrestre du Gondwana) a causé un important rabattement du niveau de la mer et une régression marine en Amérique du Nord, phénomènes qui ont mené à la première des cinq plus importantes extinctions massives de l'évolution biologique. L'île d'Anticosti faisait alors partie du bassin d'Anticosti, entité géographique plus imposante, située sur la partie est du plateau continental du paléocontinent nord-américain, et était couverte d'une mer tropicale peu profonde. Lors de la dernière extinction massive planétaire de l'Ordovicien tardif, le benthos coquiller marin du bassin d'Anticosti a connu une expansion locale considérable, ce qui nous offre une occasion idéale d'étudier les façons dont la vie marine réagit à une crise environnementale majeure. Cette étude monographique fait état des changements dans la diversité des brachiopodes (l'un des principaux groupes d'organismes marins de l'Ordovicien) de la préextinction à l'extinction.

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